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# Thermal ecology of ectotherms: the role of microclimates in climate change responses

Sylvain Pincebourde

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# HABILITATION À DIRIGER DES RECHERCHES

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**SYLVAIN PINCEBOURDE**

Le 06 Décembre 2019

## ÉCOLOGIE THERMIQUE DES ECTOTHERMES: ROLE DU MICROCLIMAT DANS LA REPOSE AU CHANGEMENT CLIMATIQUE



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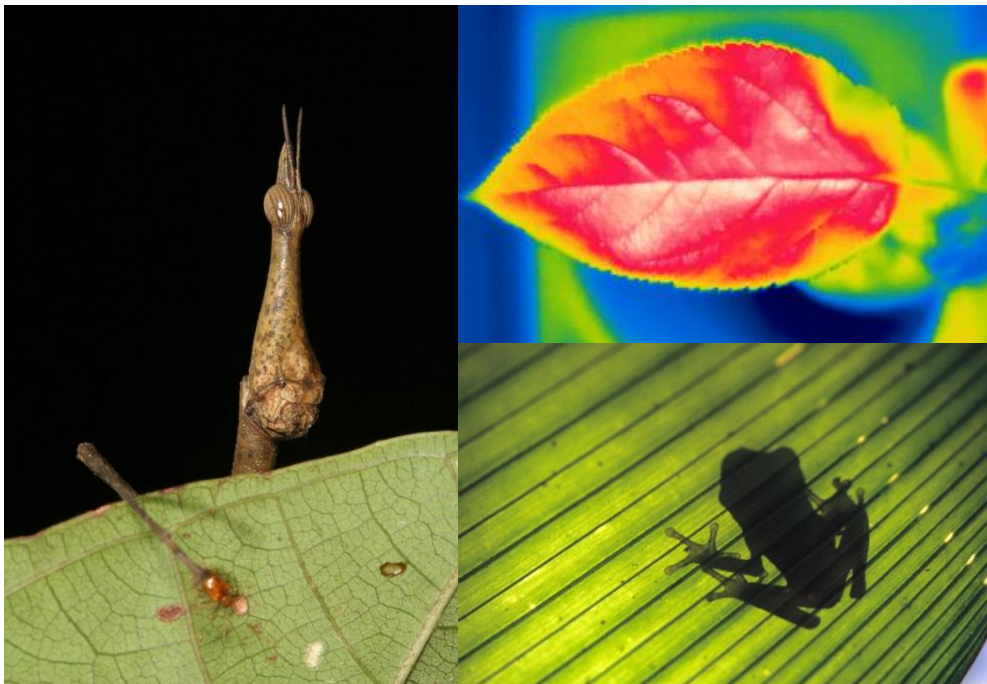
*Habilitation à Diriger des Recherches*

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Thermal ecology of ectotherms:  
The role of microclimates in climate change responses

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*Dissertation presented on December 6th, 2019*

*Discipline: Life Sciences*

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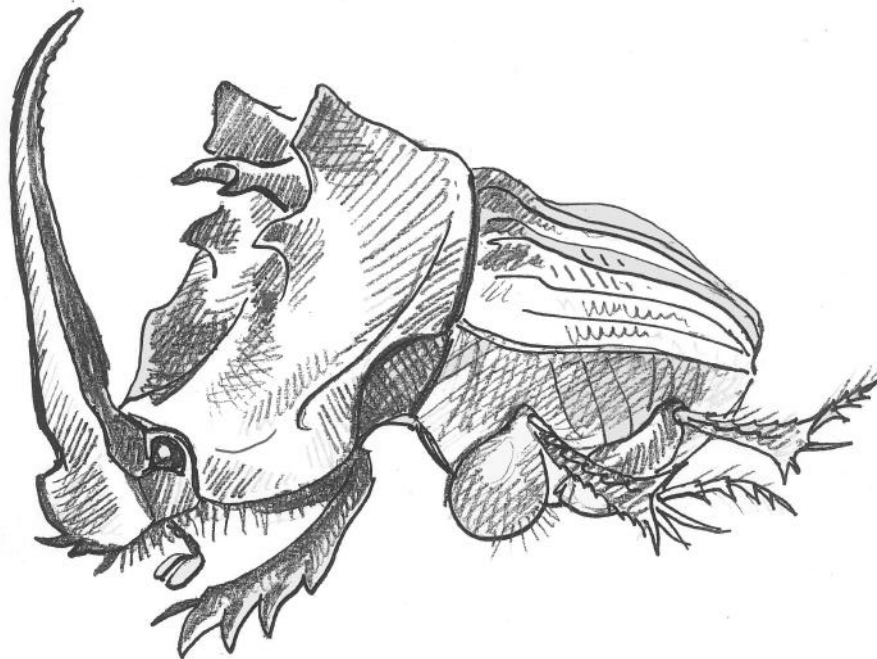
Je remercie également nos différentes tutelles. Le CNRS, et en particulier l'INEE et la délégation Centre DR08 pour leur appui financier et/ou logistique. Un grand merci à la CMG à Orléans pour les nombreux coups de pouce ces dernières années ainsi qu'à notre secrétariat, au SPV (Camille, Thomas) pour leur aide toujours aussi précieuse pour répondre aux appels à projet et à l'Université de Tours, et notamment l'Ecole Doctorale et les différents services (relations internationales, bureau de la recherche, secrétariat de l'UFR etc.).

Le parcours d'un chercheur ne peut pas se résumer à son seul parcours professionnel tant ce métier est invasif. Dans mon cas l'IRBI m'aura apporté bien plus qu'une situation professionnelle. Un grand merci à toi Christelle pour ta compréhension, ton soutien, ton appui permanent, ou encore pour juste être là à côté de moi dans tous les instants. Désolé les enfants si de façon récurrente je dois rester devant mon ordinateur au lieu de faire des activités plus fun avec vous... Enfin, j'embrasse très fort toute ma famille, et les remercie de leur patience et de leur tolérance. Désolé maman, mais papa m'a transmis son amour du travail (bien fait) quand celui-ci est passionnant ! Un grand merci à vous deux pour être toujours là.

## Preface

This dissertation was prepared to obtain the HDR ('Habilitation à Diriger des Recherches') at the University of Tours. This document covers my scientific activities since the beginning of my career during my Master and my PhD. However, my activities took another dynamics after I obtained my permanent position at the CNRS in 2009. Therefore, my dissertation mostly details the scientific projects that I led since 2009. I structured this report with four main parts: (i) My scientific pathway, to provide a concise synthesis of my CV; (ii) An overview of the field of microclimate biology, to give the fundamental concepts and knowledge; (iii) A synthesis of my scientific productions, to detail most of my published works; (iv) My research perspectives, to show where I would like to go next.

I choose to write this dissertation in English since this language is more efficient to communicate science. As a requirement from the University of Tours, a long synthesis written in French is provided in Appendix 1. The drawings and pictures that appear throughout this dissertation show species that marked my mind at some point during my career.



The largest dung beetle of South America, *Coprophaneus lancifer*. Drawing by François Feer.

# Part I.

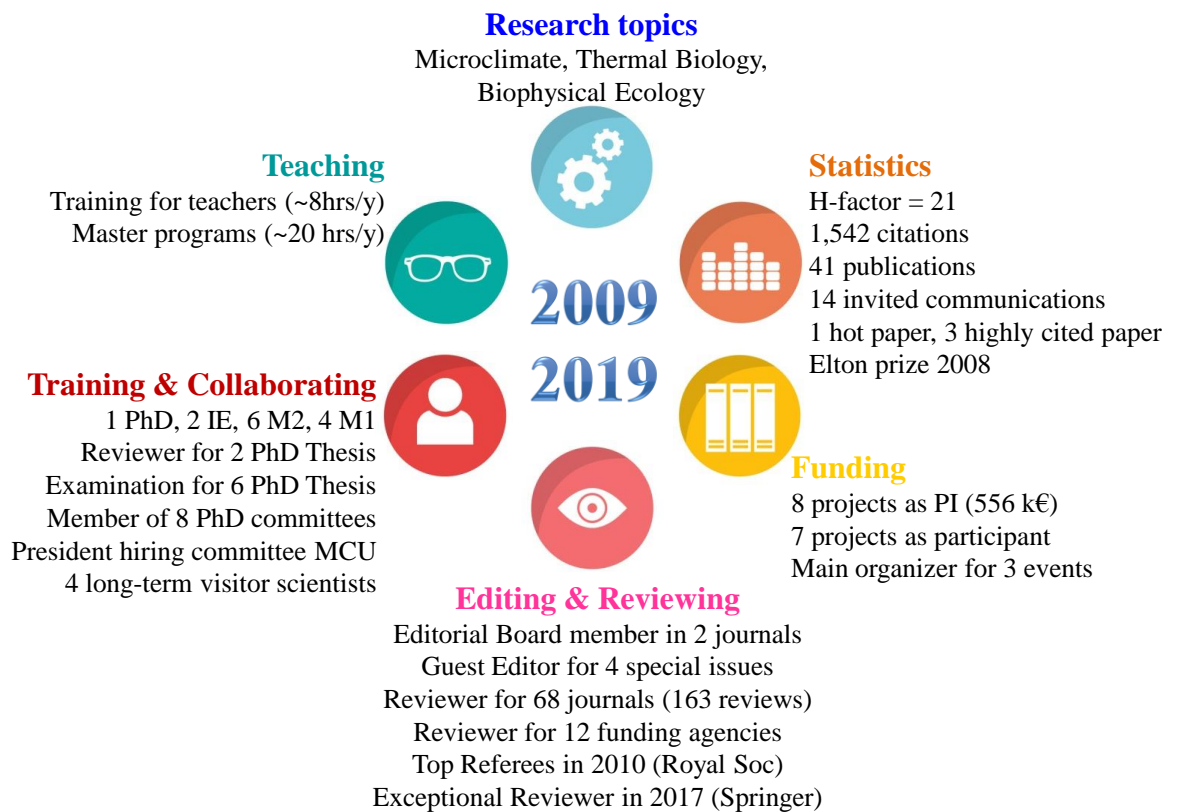
## Presentation of my scientific pathway and activities

*This section presents my scientific path and gives a synthetic view of my activities related to my research. A detailed Curriculum Vitae is given in Appendix 2.*



The Hercules beetle, *Dynastes hercules hercules*, endemic sub-species in Guadeloupe, on the edge of extinction.

## A synthetic view of my career so far



**Figure I.1.** A synthetic view of my career. The number of citations and H-factor were obtained from Google Scholar on July 18th, 2019.





## 1. My scientific pathway

### *a) Visual ecology and light environment selection in dung beetles [Master 2001-2002]*

As my scientific careers started, I met the right persons at the right moment, a chance factor that cannot be dismissed in our professional evolution. I did my Master training program with Dr. Marc Théry and Dr. François Feer at the French Museum of Natural History (Paris) on the selection of light environment and the body coloration in a family of dung beetles from French Guiana. With the great help of Prof. Jérôme Casas (GDR Physical Ecology), I had the opportunity to travel to French Guiana (South America) for field work at the CNRS Nourague field station, for two months. This field station is located in the primary forest in this tropical area. Here, I had my first chock: heterogeneity and diversity is immense at all levels. I worked on the interaction between the body coloration of Phanaeini dung beetles, their daily activity rhythm, and the quality of the light environment that they select during their activity. I discovered the discipline of physical ecology: a tasty mixture of laboratory measurements, field work and modeling to unravel the mechanisms underlying the interaction of organisms with their physical environment at a rather fine scale (both in space and time). I found my path.

### *b) Environmental biophysics of a leaf miner [PhD 2002-2005]*

Luckily, I had the opportunity to do a PhD in physical ecology right after my Master thanks to Prof. Jérôme Casas who obtained in 2002 a PhD grant to work on the thermal environment of a leaf miner species (at IRBI in Tours, France). Leaf mining insects develop inside plant leaf tissues. By feeding on leaf material from the inside, they create galleries that are called mines. Initially, the objective of the work was to describe the thermal environment within a mine and then to model it. I started by training myself with models of heat budgets for organisms (mostly for plant leaves at first). The project grew up rapidly to finally cover the eco-physiological mechanisms that influence the temperature within a mine, the consequences for the plant, the thermoregulatory potentialities for the caterpillar within a small mine, the

full multitrophic biophysical model of mine temperature and the scaling up of this model from leaf scale to canopy scale. Throughout my PhD (and beyond), the fruitful and exciting interactions I had with Prof. Jérôme Casas are undoubtedly a stepping stone in my career.

*c) Thermal ecology of a keystone intertidal predator [postdoc 2006-2007]*

Logically, Prof. Brian Helmuth was one of my referees in my PhD jury in 2005 because I basically used the same approaches (biophysical modeling of organism heat budgets) than him. We immediately co-developed a postdoctoral project on the thermal ecology of the famous ochre sea star, a keystone predator in the rocky intertidal ecosystem along the West coast of North America. Although the laboratory was hosted by the University of South Carolina, the field and lab works were all done at the Bodega Marine Laboratory, which belongs to the University of California Davis, in collaboration with Dr. Eric Sanford. Working at this huge field station was the second stepping stone in my career. Here, at the same place, I had access to the intertidal system for my field manipulations within a protected reserve and to a fancy and large laboratory with sea water running continuously to feed water tanks. The technical staff helped me to build up a unique and complex system of tens large water tank within which the tide cycle was simulated and equipped with temperature controllers for both water temperature and body temperature of sea stars when they are emersed at low tide. In addition, this postdoc corresponded to a shift from plant insect relationship to marine ecology. This change was really enriching and exciting. This postdoc lasted 2 years, and I was funded from multiple sources: from the NASA and NSF grants of Prof. Brian Helmuth and from a Lavoisier fellowship I obtained while I was already in the USA.

*d) Physical ecology of a prey-predator relationship in the litter [postdoc 2008-2009]*

I came back from the USA end of 2007 to start a second postdoc position in Tours (France) under the supervision of Prof. Jérôme Casas. The idea was to contribute to the European project CILIA (Customized Intelligent Life-inspired Arrays) which was coordinated by him, by working on the physical ecology of the prey-predator interaction between crickets and spiders at the surface of the forest litter. Again, I shift the biological model but conceptually the link with my previous

studies was obvious: the influence of environmental architecture (topography of forest litter) on interaction strength (predation rates). I had the opportunity to collaborate with a PhD student (Sylvie Morice) who was supervised by Jérôme Casas, on one of her thesis chapter which describes the 3D structure of forest litter to infer the potential influence over air flows at their surfaces. This postdoctoral period was kind of intermediate situation as I was preparing the CNRS application at the same time, with failure during three consecutive years.

*e) The key role of microclimates in a changing climate [CNRS position since 2009]*

The third stepping stone came in spring 2009, a little bit by surprise I should admit. I was ranked first at the CNRS researcher competition (for only one position) to work on the impact of climate change on individuals and populations (in the CID45 section at that time). I choose to complete my research at the IRBI, in the team led by Prof. Jérôme Casas at that time. My project focused on the impacts of climate change on multitrophic systems with a biophysical approach. More specifically, my research aimed at detailing the extent to which the microclimate of organisms plays a key role in the response of these organisms to environmental changes. I started on a plant-arthropod system but after few years I also initiated research in aquatic ecology (see below). Soon after I obtained my CNRS researcher position, I was lucky to obtain a major grant from the *Agence National pour la Recherche* (ANR) which helped me to launch my research. Several grants followed after (details below). At the same time, I met Prof. Arthur Woods during the APS conference in the USA in 2010: this meeting is another stepping stone in my early career. We got along together very nicely with lots of research ideas (see below). As always, nice and enthusiastic research is necessarily based on meeting the right persons. Now, my CNRS position allows me to integrate my experience and knowledge from various ecosystems: intertidal, plant canopies, forest litters and aquatic habitats (see perspectives). Such integration requires time to integrate data but also to build conceptual links.



## 2. Administrating and coordinating research

### a) Coordination of projects as Principal Investigator

Although I had the chance to become rapidly an independent researcher during my postdoctoral period, it was mainly in 2010 that I achieved a higher level of independency by obtaining my first significant research grants as a Principal Investigator (Table I.1). This list of projects that I coordinated can be sub-divided according to 3 categories: (i) major program in terms of funding, (ii) programs with a naturalist association as partner, and (iii) programs for international collaborations.

**Table I.1.** Summary of the funded research programs that I coordinated, arranged by year. The category is indicated near the name of the program: *i*, major funding; *ii*, program with a naturalist association; *iii*, international program.

Program	Dates	Title of the project	Amount, k€ <sup>(3)</sup>
<b>PICS (CNRS)<sup>iii</sup></b>	2016- 2018	MEGALEAF: Modeling the leaf microclimate at a global scale	9 (CNRS)
<b>APR IR (Région Centre Val de Loire)<sup>ii</sup></b>	2015- 2018	PROTECTODO: Conservation biology of Odonata in a changing climate	206 (CVL)
<b>LISEA Fondation<sup>ii</sup></b>	2013- 2018	Od'SPOT: Odonata, displacements, distribution and landscape structure <sup>(1)</sup>	50 (private funds)
<b>ANR Blanc<sup>i</sup></b>	2011- 2015	MICROCLIMITE: Connecting global climate and microclimates	260 (ANR)
<b>PNA Odonates<sup>ii</sup></b>	2012- 2015	Regional declination of the National Plan for Odonate species <sup>(1)</sup>	10 (DREAL)
<b>SPE (INRA)</b>	2011- 2013	Experimental study and biophysics of the greenhouse agrosystem <sup>(2)</sup>	20 (INRA)
<b>PEPS (INEE)</b>	2010	THERMALGAMES: Thermal games between prey and predators within the leaf microclimate	10 (CNRS)

<sup>(1)</sup> Done with the naturalist association Caudalis as co-PI.

<sup>(2)</sup> Done with a team at the Sophia-Antipolis INRA center (Alexandre Bout) as co-PI.

<sup>(3)</sup> The funding agencies are indicated in brackets: CNRS: Centre National de la Recherche Scientifique; CVL: Région Centre Val de Loire; ANR: Agence National de la Recherche; DREAL: Direction Régionale de l'Équipement, de l'Aménagement et du Logement; INRA: Institut National de la Recherche Agronomique.

- **MICROCLIMITE: the major program I led**

I coordinated the program MICROCLIMITE (Connecting global change and microclimates: the thermal budgets of a plant-herbivore interaction) from 2011 to 2015. This program was funded by the ANR (Program 'Blanc') with a global budget of 260 k€. We were two partners: IRBI and the INRA laboratory PIAF in Clermont-Ferrand (France). The team I managed was composed of permanent positions: 2 researchers, 2 Professors, 1 Engineer, and 2 Technicians. In addition, we recruited non-permanent people that I managed everyday: 1 Engineer, 1 PhD student, 2 Master students and 2 undergraduates. I established a tight coordination with the INRA partner who provided additional skills in biophysical modeling. I coordinated the links between the laboratory assays, field work and modeling tasks. I supervised the PhD student who was covered by a French Ministry Grant for his salary. Finally, my role as a coordinator also consisted in organizing meetings at different scales (from specific task meeting to general project meeting), writing reports to the ANR and developing the publication strategy.

- **The programs with a naturalist association as a partner**

Since 2012, I initiated several programs on aquatic ecology and biological conservation. In all these programs, I collaborated with the naturalist association ANEPE Caudalis. This association follows populations at the departmental and regional scales for several taxonomic groups, including Odonates (dragonflies and damselflies). We decided to work together and combine our efforts: the association knows well the sites for each species and can cover large distances to discover new populations, while I can develop manipulative experiments to understand how and why specific sites host healthy population or not. This rather rare association (in France) between a public research unit and a not-for-profit structure was applied through three different programs that are inter-connected. First, we obtained funding to *downscale* the French National Plan for Odonates down to the regional scale that matters for conservation plans (Region Centre-Val de Loire). For this program, I contacted as many structures as possible that are 'responsible' for territories susceptible to host Odonate species (associations, policy makers, managers of protected areas, etc). I interacted with them to discuss on the specific actions that can be feasible on their territories to increase the diversity of this group or to conserve rare and threaten species. A global synthesis on the current state of Odonate species

in our Region was delivered (Baeta, Sansault & Pincebourde 2012). This synthesis was jointly written with the association.

Second, we obtained private funds (LISEA Fondation) to work on the drivers of Odonate species distribution at the regional scale and more specifically on the rare species *Leucorrhinia caudalis* (Od'SPOT project). This program should deliver a book (illustrated atlas) on the distribution of Odonate species in the department in 2020. A total of 5 Master students were included in the project. We also obtained a prize in 2013 for this combination of a public research organization, a naturalist association and a private Mécénat, given by the Ministry of Ecology (Trophy for corporate sponsorship, 2013).

Third, in line with the Od'SPOT project above, I obtained funding from the Région Centre Val de Loire to work on the thermal ecology of dragonfly larvae (PROTECTODO project). The team that I coordinate is composed of 2 Professors, 1 Technician and the naturalist association. In addition, I hired an Engineer on this project, and I supervised 3 Master students. This program also includes several Loire Castles as partners to assess the extent to which the parks of these castles can be managed to increase their diversity of Odonate species.

- **Leading an international program**

Since 2016, I coordinate a project (MEGALEAF) as a PICS program for international collaboration. The PICS are a tool supported by the CNRS to promote international collaborations that are already in place but need support to grow. I develop this project with the University of Montana (Prof. Arthur Woods) and the INRA PIAF laboratory of Clermont-Ferrand (Dr. Marc Saudreau). The funding is to support short-term travels among us and to organize an international workshop at some point. I managed to use this funding conjointly with other opportunities to increase our capabilities, for example by combining a PICS meeting with the invitation of Arthur Woods to an international conference that we organized in Tours. A report is provided every year to the CNRS which decides whether or not they continue to support our program (up to 3 years).

- **Short and long term visits of professors for collaborations**

In 2012-2013, Prof. Arthur Woods (University of Montana) came at the IRBI to collaborate with me during a full year sabbatical supported by the University of

Montana. We managed to have a total of 3 months as a status of invited Professor at the University of Tours as a complement. The decision of Arthurs Woods to come in Tours followed our first meeting in 2010 at the American Physiological Society in Denver, the starting point of our collaboration which generated 7 publications as of today.

More recently, in 2019, Prof. Michael Dillon (University of Wyoming) visited me at the IRBI with the status of invited professor at the University of Tours. This visit followed my own visit (in 2018) to the Grand Tetons field research station that Michael Dillon supervises, during which we initiated a field experiment on the influence of insect body size on insect body temperature at the surface of plant leaves. His stay in Tours for a month allowed us to pursue this project.

At the same time in summer 2019, Prof. John Terblanche and Prof. Susana Clusella-Trullas (University of Stellenbosch, South Africa) came at IRBI for 4 months for a short-term sabbatical supported by the University of Stellenbosch. We developed a project that was initiated during our meeting at the Symposium on Insect-Plant Relationships that we organized in Tours in 2017. We worked on oxygen limitation galls initiated by insects on plant leaves, as function of gall size and temperature within the gall.

#### *b) Supervision of students*

Supervising and training students is an important part of a researcher path. My own way is to focus on a single Master-level student every year. Since 2009, I supervised two engineers, five 2nd year Master students, and 4 undergraduates. When I supervise and train students, I take care of giving them autonomy but at the same time I supervise tightly the development of experimental design and early developments of the study program. I also want to give the opportunity to students to write a publication with their results, but as of today only two publications are significantly advanced with these students as first author. In the future, I will give more inputs during the early developments of writing the draft (e.g. right at the end of the training program before the student leaves) to finally be successful at publishing with these students as first author.

I co-supervised one PhD student (Robin Caillon, 2011-2015), leading to one publication with the student as first author, one publication as first author in revision, and two publications accepted as co-author. Then, I collaborated directly with three



PhD students who were supervised by other colleagues. For each student (Frédéric Bernard, Emile Faye and Estefania Quenta), I was involved in one of the thesis chapter, leading to publications. Beyond *official* supervision or direct collaboration, I am always keen on letting the door open for any student from the team and beyond who needs help, from simply reading manuscripts to discussing results or experimental designs.

*c) Expertise and committees*

I served as an expert for 12 different funding agencies since 2009. I was contacted by both French and foreign agencies including the FNRS (Belgium), the CONICYT (Chile) and the American NSF (in 2009 and 2017), and more recently the ERC and the MacArthur Fellowship for example. This activity differs much from reviewing a regular scientific paper. In particular, the NSF has well-identified guidelines and expectations from the experts. For all these agencies but the NSF, I wish I had a feedback in terms of whether or not the project I assessed was retained. In the same spirit, although not related to funding, I was part of the Nature Reader Panel for a full year (2010-2011): as an *expert reader*, I had to give my opinion on the structure and content of each issue of the journal *Nature*. This task helped me to refine what I like to read and what I think is unnecessary when speaking about science, from the regular scientific article to the media-sharing piece written in a smooth language. During this period, I realized that journalists can largely modify what we - as scientists - intend to explain. A totally surprising and unconventional result for the journalist may quite often be toned down by the authors themselves in the original publication. I was myself confronted with this problem when the few publications I have on the thermal ecology of the famous ochre sea star *Pisaster* started to make the buzz in the social media and the classic paper and radio media. I would not recommend reading some of these newspapers covering my own research!

Since 2013, I am a member of various committees with different aims. I am member of the Departmental Commission for Nature, Landscapes and Sites, in particular for all questions related to biodiversity. This official public commission takes position and decision on diverse demands relative to, for example, a change in the status of protection of particularly sensitive natural sites, the importation of exotic animals, the need to manipulate protected species for scientific purposes, etc. In addition, I am the correspondent for my Institute (IRBI) at the MIDI network (*Les*

*rendez-vous des Milieux et de la Diversité pour une gestion durable des Ressources naturelles et de la Biodiversité*). This regional network establishes the link between all researchers working on any aspects of biodiversity, including the ecological sciences, the social and political sciences, and the geography or geology. As part of the Bureau of this network, I am in charge of communicating to the IRBI all information relative to the activities of the network. I also take part to organizing events in the name of the MIDI network. For example, I took part of the scientific and organizing committees of the international conference on climate change and water that we organized in February 2018. This conference brought together about 120 participants including both scientists and policy-makers. Finally, from 2013 to 2017 I was a member of the bureau of the EPIARCH network (Epidemiology and Architecture of plants) which was supported by the INRA. This network was much more specific than the MIDI network scientifically, and my tasks differed: in the network EPIARCH, I served as expert on entomology, architecture of plants and microclimatic questions. We had regular workshops and meetings to discuss what was done in this field, and mostly to develop new integrated proposals to obtain funding.

Finally, I regularly take part to PhD committees (eight since 2010)<sup>1</sup>. I was contacted to provide expertise on very different themes including thermal biology (on a fungal pathogen), aquatic ecology (on Odonates in the South of France) and on entomology (biodiversity in vineyards). In addition, I did jury service in six different PhD defenses, including that of my own student Robin Caillon.

*d) Team manager since January 2018*

My contribution to administrating research moved a step forward in 2017, and officially in January 2018. I become the head of the new team INOV (INteractions between Organisms and their enVironment) at the IRBI. As such, I manage, administrate and represent a team composed of (permanent positions) 3 Professors, 4 assistant Professors (*Maître de conférence*), and 3 Technicians. The team also includes several graduates and undergraduates, as well as non-permanent staffs. From a scientific point of view, the team INOV deals with four topics: thermal ecology, physical ecology, sensory ecology and the fourth theme is based on these

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<sup>1</sup> The PhD committees are supposed to happen two times during the three years of a PhD in France.

previous mechanistic themes to advance societal questions such as ecological impacts of climate change, biological invasions and agroecology. My task as a leader of the team INOV is to animate the group, to facilitate the interaction between the members especially given that we all work on contrasting aspects of organismal biology, to defend the interests of the team during the committees of the Institute, to administrate the team (funding, organization of meetings etc.), and to ease the transfer of information inward and outward the team.



### 3. Valorizing research

#### a) Peer-reviewed publications

Since 2004, I have published 41 peer-reviewed articles in 29 different international journals. I am the lead author for 16 papers and last (senior) author for 14 papers. I never published without co-authors: the number of co-authors ranges between 2 and 12 (excluding the road map paper, Giron et al. 2018, published in *Entomologia Experimentalis y Applicata* which has 22 co-authors). The mean impact factor (IF) is 3.97 and the median IF is 3.10 (Table I.2). The number of articles published every year has increased markedly in 2012 (year of the *Ecology Letters*). This is due to an increase in number of papers every year, since 2012, in both high impact journals (*PNAS*, *Ecology Letters*, *Global Change Biology*, *Ecological Monographs*) and more specialized journals (Table I.2). A total of 5 papers were published in special issues and one in a virtual special issue. The most striking characteristic of my publication list is the diversity of disciplines: my papers fall in 11 ISI categories (Multidisciplinary sciences, Ecology, Biology, Plant Sciences, Forestry, Zoology, Entomology, Oceanography, Marine and Freshwater Biology, Environmental Sciences and Meteorology & Atmospheric Sciences). This observation reflects the variety of research themes I have covered since 2004, associated with the various biological models I studied (plants, insects, marine invertebrates), rather than a truly multidisciplinary approach which would have generated publications in contrasting fields from mathematical, physical or social sciences.

**Table I.2.** List of peer-reviewed publications since 2004 (N=41), arranged by ISI category and by IF (2018). The category *Marine Sciences* merges the ISI categories *Oceanography* and *Marine and Freshwater Biology*. The indexes *I2* and *I5* are shown in red when they are above 1 (i.e., higher impact than the average publication for the given journal) and in blue when below 1 (i.e., lower than average impact). Values between brackets are only estimates because of missing data (recent papers).

Category / journal	Year	IF 2018	Author rank	Index <i>I2</i>	Index <i>I5</i>
<b>Multidisciplinary Sciences</b>					
PNAS	2019	9.6	1/2	na	na
<b>Ecology</b>					
Ecology Letters	2012	8.7	1/4	1.31	3.31
Ecological Monographs	2006	7.7	1/2	0.57	1.68
	2017		2/3	(1.95)	na
Functional Ecology	2012	5.0	1/2	3.11	7.42
	2014		5/5	1.95	(5.83)
Ecology	2005	4.3	2/6	2.9	7.72
	2009		2/12	0.21	0.65
	2015		1/2	4.33	(6.41)
Oikos	2005	3.5	3/3	1.28	2.81
The American Naturalist	2009	3.9	1/3	1.48	4.23
Ecology & Evolution	2018	2.4	3/3	na	na
	2018		2/4	na	na
Journal of Tropical Ecology	2005	1.2	2/2	3.65	11.15
Rethinking Ecology	2019	na	3/5	na	na
<b>Environmental Sciences</b>					
Front Ecol & Environment	2016	10.9	1/4	0	na
Global Change Biology	2013	8.9	3/3	6.16	17.80
Agr and Forest Meteorology	2019	4.2	7/9	na	na
<b>Zoology</b>					
Journal of Animal Ecology	2007	4.4	1/4	1.08	2.71
Behavioral Ecology	2008	2.7	2/3	2.39	4.18
Integrative & Comparative Biology	2013	3.1	2/5	2.03	2.91
	2016		1/4	6.45	na
	2016		1/2	2.58	na
	2016		8/8	6.45	na
<b>Biology</b>					
Journal of Exp Biology	2013	3.0	1/3	1.70	3.30
Journal of Thermal Biology	2015	1.9	3/3	18.16	(32.31)
	2016		3/3	8.94	na
<b>Entomology</b>					
Journal of Insect Physiology	2006	2.9	1/2	1.39	3.27
	2015		6/8	1.10	(2.53)
	2016		1/2	4.54	na
Insects	2018	2.1	3/3	na	na
Journal of Insect Conservation	2019	1.3	5/5	na	na
Entomologia Exp App	2018	1.6	22/22	na	na
	2018		3/3	na	na
Physiological Entomology	2004	1.4	2/3	2.21	9.05
<b>Plant Sciences (incl. Forestry)</b>					
Plant cell & Environment	2006	5.6	1/5	0.43	0.87
	2017		6/6	(1.07)	na
Trees - Structure & Function	2013	1.8	2/6	2.34	5.93
Advances in Botanical Res	2017	2.3	1/7	(3.06)	na
<b>Marine Sciences</b>					
Limnology & Oceanography	2008	4.3	1/3	4.43	10.62
J Exp Mar Biol Ecol	2012	2.4	3/4	1.07	4.15

Legends: PNAS: *Proceedings of the National Academy of Sciences USA*; *Front Ecol & Environment: Frontiers in Ecology and the Environment*; *Agr and Forest Meteorology: Agricultural and Forest Meteorology*; *Journal of Exp Biology: Journal of Experimental Biology*; *Entomologia Exp App: Entomologia Experimental et Applicata*; *J Exp Mar Biol Ecol: Journal of Experimental Marine Biology and Ecology*. The indexes cannot be calculated for the papers published in 2018 and 2019 (noted as 'na').

In June 2019, I was acknowledged by the journal *Integrative and Comparative Biology* because I was author on two publications (Pincebourde et al. 2016; Dillon et al. 2016) that were ranked in the top 3 most cited publications from the previous 2 years (29 and 25 citations, respectively). In other words, these publications contributed the most to the increase in the journal IF in 2018. From this observation, I wondered to what extent, in general, my publications are making a difference for the journals I publish in. Are my publications more cited than average in these journals? For each publication, I developed and calculated the indexes of impact **I2** and **I5** which corresponds to the impact of a publication relative to the IF (typically 2 years) and the 5 years-IF, respectively (Table I.2). Such indexes do not exist in the literature as far as I know. These indexes were calculated as follow:

**I2** = [total number of citations the given publication, published in year n-2, obtained as of year n] / [IF of the journal for year n and published by ISI in year n+1]

**I5** = [total number of citations the given publication, published in year n-5, obtained as of year n] / [IF of the journal for year n and published by ISI in year n+1]

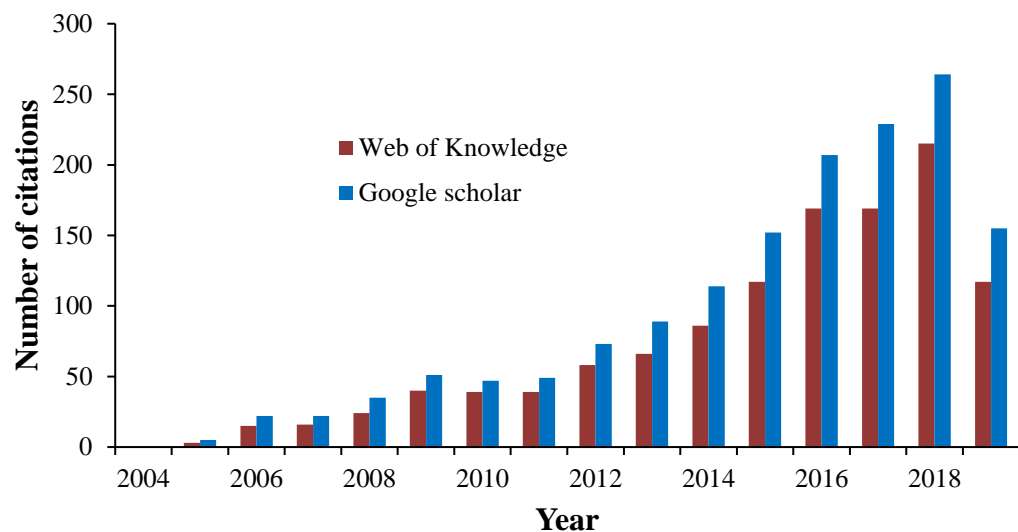
These indexes equal 1 when the paper had the same impact than the averaged paper published in this journal (i.e., number of citations equals IF). An index below 1 suggests a lower impact while a value above 1 means a higher impact. For example, my publication in *Ecology Letters* was published in 2012 and obtained 14 cites by end of 2014. The 2014 IF of this journal (therefore, based on cites for years 2012 and 2013) was 10.689. For this case study, **I2** = 14/10.689 = 1.31, and **I5** is 39 (cites for years 2012 to 2017) divided by 11.775 (the 5 years-IF of the journal for 2017), which gives 3.31. Therefore, my paper in *Ecology Letters* had the same impact over the short term than the averaged paper published in this journal (**I2** close to 1). By contrast, my paper impacted the community thrice more than the averaged paper in this journal over 5 years. In general the I5 index is higher than I2, confirming (at my level!) that early citations underestimate future impact (Wang et al. 2013). It should be stressed that these indexes quantify the 'success' of a publication relative to the

average of a given journal: two publications with the same number of citations have different indexes because they are published in two journals with contrasting IF. Then, these indexes cannot be accurately calculated when they are recent (less than 2 years or 5 years for the indexes **I2** and **I5**, respectively). In addition, this calculation is only based on IF and number of citations. The real impact of a publication in a field should be seen well beyond these two metrics. Nevertheless, these indexes allow me to estimate the degree to which my publications are *diffusing* (short-term impact) versus *infusing* (long-term impact) the field.

Overall, these indexes indicate that my publications tend to impact over the long term rather than short term. Although there is a large variability, the mean **I5** (5.46) is higher than the mean **I2** (3.25) when excluding the recent papers for which years are still missing to have a final estimate of the indexes. In addition, the number of publications with an index near 1 (average impact) is higher for the index **I2** (N=9) than for **I5** (N=1). This result shows that my scientific results are infusing the community (i.e., it may take time to assimilate or accept these results) rather than diffusing (i.e., results are taken immediately). Amazingly, the best indexes are obtained for publications in journals with moderate to good IF, and not necessarily in journals with the highest IF. For example, the highest **I2** is obtained for a publication in the *Journal of Thermal Biology* (IF 1.9). This publication received many citations immediately after it was published (mostly because it was visible on-line first for more than 6 months before it was published in an issue). Now, the rate of citation is stable every year, leading to a theoretical **I5** of 32.31 (but this value will be known in 2 years from now). Therefore, this publication (Woods, Dillon & Pincebourde 2016) was rapidly diffusing, and it continues to infuse the community in this field of climate change biology. Again these indexes are relative to the given journal performance. My publication in *Global Change Biology* gets twice more citations every year than the paper in *Journal of Thermal Biology* above, but it has a lower **I2** (6.16 vs. 18.16).

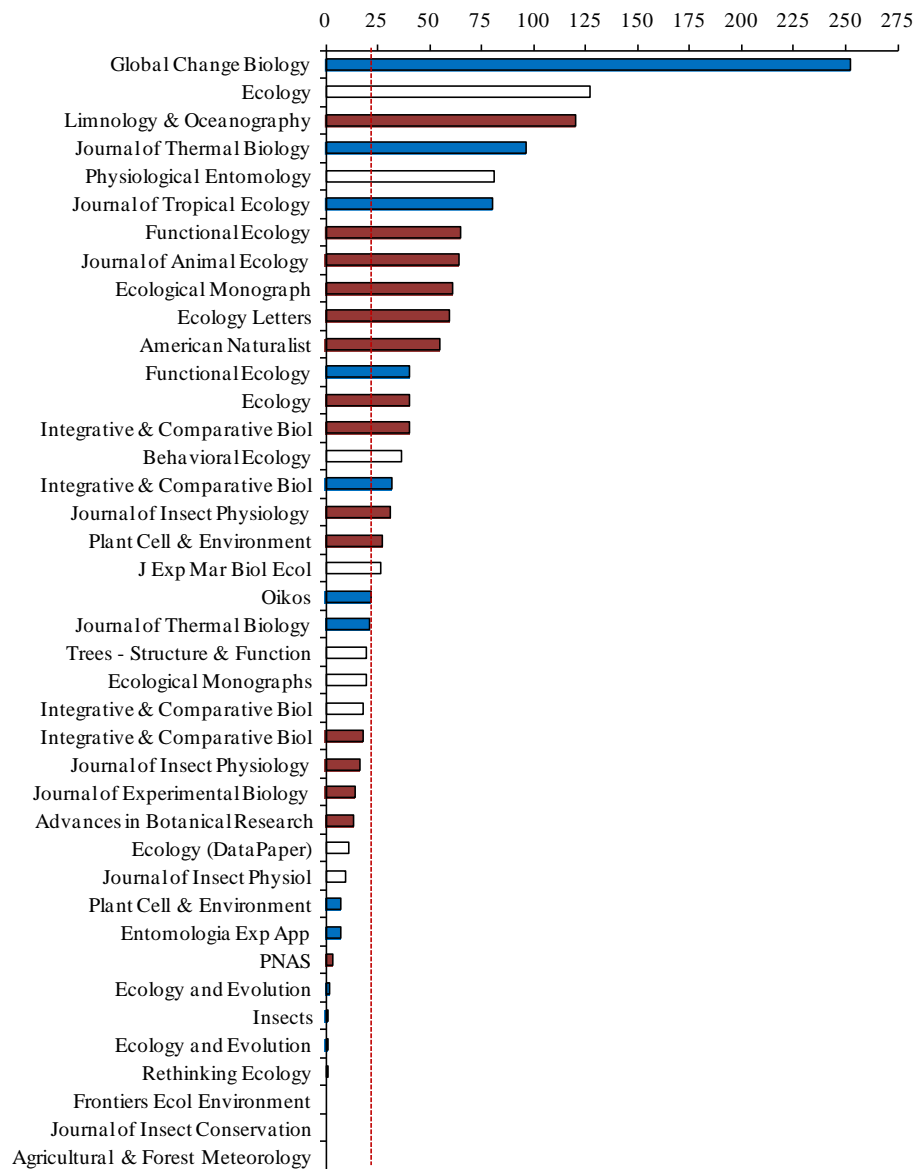
The absolute number of citations is useful to determine how well-balanced the profile of a researcher is. The number of citations increased regularly every year for my publications (Figure I.2). Overall, my publications have more than 1,542 citations with an H-factor of 21 (in Google Scholar; in Web of Knowledge, H-factor = 18). Therefore, I have 20 publications above and below my H-factor, suggesting a relatively balanced profile. However, at least 3 publications are *over-cited* compared

to the others (Figure I.3). Indeed, there are more citations above my H-factor (934) than below it (240), indicating that I have a profile slightly unbalanced with few publications that are overly cited compared to the others. This unbalance is mostly caused by the paper in *Global Change Biology* (Potter, Woods and Pincebourde, 2013) which has >250 citations. Otherwise, 4 publications have about 6 citations per year. Although the success of our paper in *Global Change Biology* (Microclimatic challenges in global change biology) was expected, other successes were more surprising (e.g., Woods, Dillon and Pincebourde in *Journal of Thermal Biology* 2015). In my experience, the success of a paper does not really depend on the level of co-authoring and could be independent from the IF of the journal. A higher IF could help however as it means that the journal may have a higher visibility.



**Figure I.2.** Number of citations per year since 2004 (as of July 18th, 2019) according to the two main sources, Web of Knowledge (red bars) and Google Scholar (blue bars).





**Figure I.3.** Ranked number of citations for the 41 peer-reviewed publications as of July 18th, 2019 (source: Google Scholar). Color bars represent publications as 1<sup>st</sup> author (red bars), last author (blue bars) or co-author (white bars). The red dotted line shows my H-factor (21).

*b) Presenting communications in scientific conferences*

As of today, I gave 41 oral and 13 poster communications in international and national conferences. My *strategy* is to present my work at a big ecological conference about every 2 years (e.g., ESA, BES, SICB, APS, Our Common Future), and to participate to more specialized meetings otherwise, which could be national (e.g., eco-physiology colloquium) and international (e.g., SFEcology, SWGEN,

FSPM, ECA) events. This scheme is obviously modulated by opportunities (e.g., invitations) and by practical issues (e.g., funding, calendar issues, etc.).

Among the 41 oral presentations of my work, 14 were invited communications. I am regularly invited to conferences since 2012 (11 invitations since 2012). The type of invited conference varies widely, including: large annual meeting of famous societies (SICB, BES), specialized international symposium with small but high-level audience (STUDIUM on insect reprogramming plants), specialized international workshop on climate issues (SWGEM), and invitations to present to a lab or university (e.g., Univ Montana, Trinity College, UC Davies). Some of these invitations were productive. My participation to the Symposium *Beyond the mean* (organized by Arthur Woods and Michael Dillon), at the SICB meeting in 2016, generated 3 publications in the journal *Integrative and Comparative Biology*. My presentation at the STUDIUM conference led to an article in the *Journal of Insect Physiology* (special issue).



## 4. Structuring research

### a) *Editing and reviewing*

I am Handling Editor for *Oecologia* and Associate Editor for *The American Naturalist*. Although the two titles differ, the job remains the same. I give a brief description of my experience in these two journals below.

Since January 2014, I am Handling Editor for the journal *Oecologia*, in the category Terrestrial Invertebrate Ecology (under supervision of Prof. Roland Brandl). This journal has 6 categories, each with about 20-30 handling editors working for their respective Editor-in-Chief. Therefore, each handling editor is relatively less solicited compared to other journals, which have fewer agents to handle submissions. Since 2014, I handled 39 papers for *Oecologia* (i.e., about 6 manuscripts every year). I am also Associate Editor for *The American Naturalist* since November 2018 (reporting mostly to the Editor Russell Bonduriansky, and to lesser extent to Editors Daniel I. Bolnick and Alice A. Winn). I have already handled 10 papers, suggesting (by extrapolation) an average of ~15 papers per year (another scale compared to

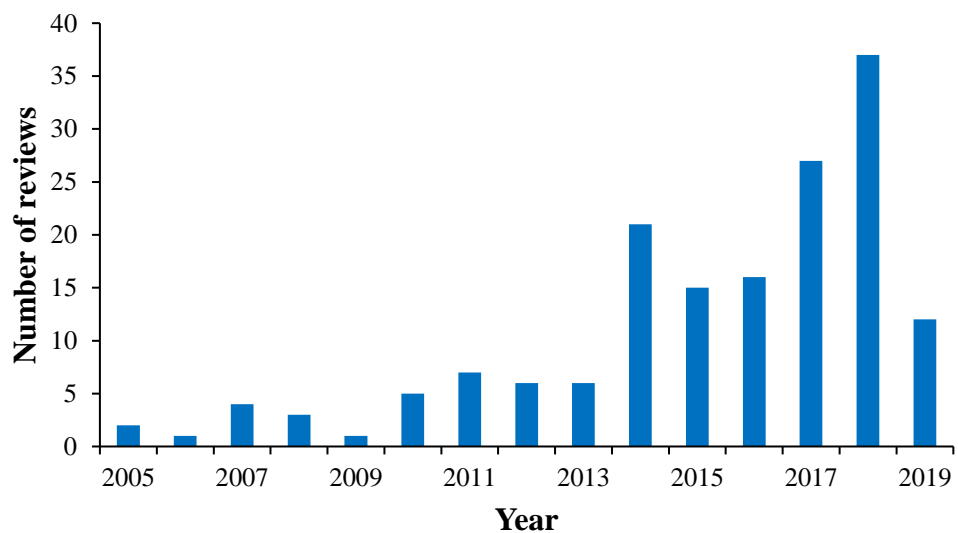
*Oecologia*). *Am Nat* requires that the Associate Editor provide extensive comments to authors, based on both reviewers' comments and their own reading. It seems that the authors are in general quite pleased to get such detailed feedbacks, whatever the paper is accepted or not.

For the two journals, the main difficulty is to find reviewers: the rate of decline is high (on average, 5-10 contacts to get 2 reviewers, with a record of 22 persons contacted to finally have only one reviewer in *Oecologia*). Another constraint in *Am Nat* is that they ask us to provide a list of potential reviewers that is balancing the sex ratio and career stage (Senior, Junior). The main reason for declining (the reason provided) is that people are swamped with others reviews and activities (fieldwork is a frequent reason for declining). Rarely, the contacted scientist never responded to the solicitation, or accepted to review the paper but never sent the review back (one case). In addition, late reviews are finally anecdotic. Therefore, the main constraints on reviewing appear to be the charge of work of everyone, which makes people less prone to accept reviews. One strategy to circumvent this constraint is to solicit both senior and junior experts at the same time. My experience suggests that the best balance of reviews can be obtained when the reviewers are a mixture of senior (professors, tenures etc.) and junior (postdoctoral researchers etc.) scientists. Overall, junior experts are faster to respond to solicitations, and less likely to decline the invitation to review.

The journal *Oecologia* also solicits Handling Editors for other tasks. The journal has the entry category named Highlighted Student Research, which puts in front of the journal (and open access) the articles published as part of a PhD dissertation. Every year since 2017, I am involved in the committee to select the best paper published in this category (N=9-15 papers every year): the Hanski Award (in honor of Ilkka Hanski who died in 2016) for publications in all areas of animal ecology. Such a paper should be relevant to animal ecology in general, and it should stand for innovation and thoughtfulness in concept, and care and rigor in execution. Editors-in-Chief make their choice based on the recommendations from each committee member.

Reviewing is another important part of my scientific activities. As of today, I served as reviewer for 68 different journals (with 163 reviews) from diverse disciplines (Ecology, Biology, Entomology, Zoology, Multidisciplinary Sciences, Environmental Sciences, Meteorology and Atmospheric Sciences, Oceanography,

Marine and Freshwater Biology, and Horticulture). The dynamics of the number of reviews per year shows two periods (Figure I.4) with less than 7 reviews every year in the period 2005-2013 (mean 3.89) and 15 to 37 reviews every year since 2014 (mean 21.33). I accept almost all solicitations (decline rate of 8%). Therefore, currently, I review almost 4 manuscripts for each article I publish, which is a bit more than the mean number of reviewers I had on my own manuscripts (so I can probably start declining more than 8 %!). I always try to return honest, constructive, friendly, timely and carefully written reviews to the best I can. I always accept to read the revised versions of the manuscripts. These values were probably the reasons for the journal *Biology Letters* to nominate me among the 10 Best Referees for year 2010. Note however that this nomination in 2010 did not influence the number of solicitations I had every year (Figure I.4; compare periods 2010-2013 and after 2014). Later, in 2017, I was nominated as an ‘Exceptional reviewer’ among Springer journals for the reviews I did for *Oecologia* (these nominations were suggested by the Editors of these journals).



**Figure I.4.** Number of reviews per year from 2005 to July 2019.

*b) Organizing events*

I contributed to community service by organizing two workshops (HETEROCLIM, Ecologia termica) and by participating to the organization of three other events (SFE 2010, CBI 2016, SIP2017). Here I detail the two workshops that are the most significant.



**International workshop HETEROCLIM:** The response of organisms to climate change in heterogeneous environments.

*Date:* 10-14 June 2014, Loches, France.

*Main organizer:* Sylvain Pincebourde.

*Scientific committee:* Sylvain Pincebourde, Olivier Dangles (IRD, Ecuador), Jérôme Casas (IRBI) and Brian Helmuth (Northeastern Univ, USA).

*Participants:* 21 invited speakers (including 14 non-French) and 32 participants (including 16 non-French). <http://casas-lab.irbi.univ-tours.fr/heteroclim.html>

*Funding:* ANR, IRD, INEE, Conseil Régional Centre Val de Loire, University François Rabelais.

Scientists have developed sophisticated methodologies to predict the ecological impacts of climate change. These methods, however, are challenged by scaling issues. Climate models predict temperatures for spatial units of 1 km<sup>2</sup> on average, which is much larger than the body size of organisms. These methods neglect the spatial heterogeneity in temperature within the smallest scales that are pertinent to organisms. Nevertheless, recent studies showed that, at least theoretically, organisms such as insects and reptiles could buffer part of an increase in temperature by moving locally. It is not clear how this spatial heterogeneity will evolve during global change. The objective of the workshop HETEROCLIM was to establish a state of art on the processes linking the climate heterogeneity at various spatial scales and the responses of organisms. The project needed to include knowledge from various disciplines including atmospheric sciences, biogeography, thermal biology, animal and plant ecophysiology, biophysical ecology, modeling and biostatistics. The workshop was split into 3 sessions: (i) How do we connect global change and local or microclimatic changes?, (ii) How do we predict the performance of organisms in fluctuating environments?, and (iii) How do we model the

distribution of organisms in space under a changing climate? Finally, a fourth session was devoted to thinking about perspectives and what are the future challenges on each of the above questions. This workshop was successful in attracting among the best world leading scientists in this field (Table I.3).

**Table I.3.** Summary of the 21 invited speakers present at the workshop HETEROCLIM (June 2014).

Session #	Name	Country	Keyword(s)
<b>Introduction</b>	Michael Angilletta	USA	Thermal adaptation
<b>1</b>	Christian Körner	Switzerland	Bioclimatology, climate envelop
<b>1</b>	Solomon Dobrowski	USA	Climate refugia, climate downscaling
<b>1</b>	Mathieu Vrac	France	Climate downscaling
<b>1</b>	Colin Prentice	UK	Biosphere - atmosphere interactions
<b>1</b>	Mark Denny	USA	Spatial scaling and biophysical ecology
<b>1</b>	Dennis Allard	France	Biostatistics & spatial processes
<b>2</b>	Volker Loeschcke	Denmark	Genetics of thermal tolerance
<b>2</b>	Joel Kingsolver	USA	Thermal sensitivities
<b>2</b>	David Grémillet	France	Eco-physiology in a warming world
<b>2</b>	Carlos Navas	Brazil	Thermal ecology in altitude
<b>2</b>	Sylvain Pincebourde	France	Thermal ecology
<b>2</b>	Arthur Woods	USA	Ecological and environmental physiology
<b>2</b>	Olivier Dangles	Bolivia	Thermal landscapes
<b>3</b>	Brian Helmuth	USA	Biophysical ecology
<b>3</b>	Michael Kearney	Australia	Mechanistic niche modeling
<b>3</b>	Lauren Buckley	USA	Mechanistic vs. correlatives niche modeling
<b>3</b>	Wilfried Thuiller	France	Species distribution models
<b>3</b>	Miguel Araújo	Spain	Statistical niche modeling
<b>3</b>	Lisandro Benedetti-Cecchi	Italy	Ecological variance
<b>3</b>	Jonathan Lenoir	France	Plant macroecology

The HETEROCLIM workshop was the opportunity to initiate a new network on the topic of global change biology. This topic is expanding since a decade or more, and this workshop helped to position French scientists and in particular the CNRS, IRD and the University François Rabelais, at the forefront of this research. This network was at the heart of a proposal that I led and submitted to the CESAB (FRB) in 2014 and 2015, but the project was not retained. I am now thinking about other funding options at the European level (see *Part IV: Research perspectives*).



**'Ecología térmica' workshop:** workshop on thermal ecology for South American scientists and students.

*Date:* 24-25 June 2015.

*Main organizers:* Olivier Dangles and Sylvain Pincebourde.

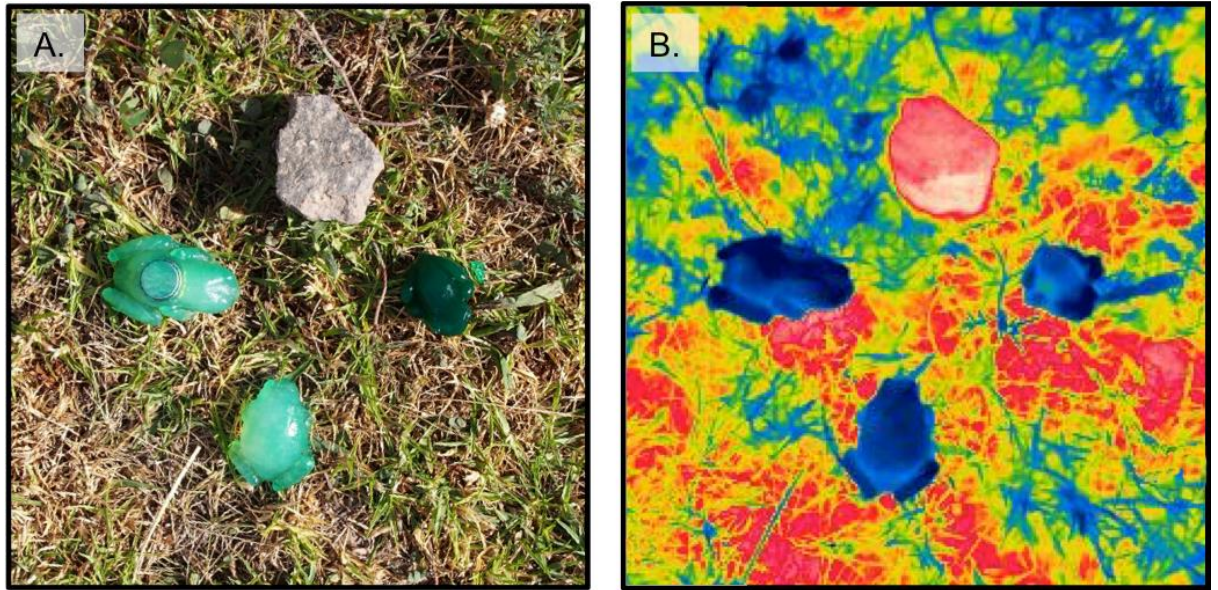
*Contributors:* François Rebaudo, Emile Faye, Rommel Montufar, Erika Páez.

*Participants:* 10 Ecuadorian students and scientists.

*Funding:* Pontificia Universidad Católica del Ecuador (Quito), ANR.

The field of thermal ecology has regained large interest since 10-20 years because of the urge to provide answers to the global change challenge. In the context of skill acquisition by people in developing countries, we thought appropriate to organize a workshop on thermal ecology for students and scientists in Ecuador. The format was a training program with courses, field work and computer training with a small number of attendants (20). The objective of this workshop was to teach thermal ecology to students and scientists of Ecuador. The workshop was split into 3 steps: (i) the theoretical background and generalities in thermal ecology (course that I gave), (ii) techniques and methods in thermal ecology with a field trip in the Andes to learn how to use infrared cameras (course given by Emile Faye; Figure I.5), and (iii) methods to analyze thermographic images with a code in R (course given by François Rebaudo). Finally, among the few students that attended the workshop, two became students at the Insect Biology Research Institute in Tours. Erika Páez did her Master training program with me on the thermal ecology of Sphingids, and Estefania Quenta did her PhD with Prof. Jérôme Casas and I contributed to her third chapter on the thermal ecology of dragonfly larvae.





**Figure 1.5.** Exercise to illustrate the importance of evapotranspiration on the body temperature of frogs in tropical environments. The field training program helped a researcher to validate its agar model of frog body temperature: an iButton was inserted into the frog-shaped piece of green agar (A) and the thermal camera was used at the same time to record surface temperature when in full sun (B). A rock was used as a reference for a highly absorbing surface. Credit: Emile Faye and Sylvain Pincebourde; Figure reproduced from Emile Faye (2015).



## 5 Teaching and diffusion actions

### a) Teaching at the university

As a CNRS researcher, teaching is not mandatory although this activity is largely encouraged. I think that it is important to keep this link with students for several reasons: (i) it is a good way of detecting the best and promising students that I can later train during a research program; (ii) teaching is a nice way to enlarge my own vision on my research field in general, especially when it comes to communicate on climate change issues; and (iii) teaching is a powerful channel through which we can start to change the way people think about global change and biodiversity in general (although, the students I teach are obviously already sensitive to such issues as they are in a biology path). My teaching record greatly depends on opportunities. Therefore, I teach only few hours to two different Master programs at the University of Orleans and the school AgroParis Tech on the importance of plant

architecture in ecological research in the context of climate change. And I teach to a larger extent to the Master program (years 1 and 2) of the University of Tours (about 20 hours every year since 2013). Here, the charge allows me to develop a course on thermal ecology of organisms with a special emphasis on the importance of ecophysiological knowledge when attempting to predict the ecological impacts of climate change. In particular, I developed a training course on the use and misuses of thermal imaging during which students had the opportunity to manipulate an infrared camera. This training was particularly appreciated by students (according to the satisfaction survey). Overall, my aim is to have students realizing that the IPCC prediction of warming may not necessarily give directly the amplitude of warming that organisms will experience within their microhabitat because of the microclimatic and behavioral (thermoregulation) issues.

*b) Training teachers*

Early in my career I had the opportunity to operate directly in schools with kids around 10, simply to talk about the importance of biodiversity with insects as support. I realized that in one shot I can influence about 30 kids who are especially receptive by nature to the questions related to biodiversity conservation. And by training 30 teachers, I can influence (potentially at least) 30 times 30 = 900 kids in one shot! Training teachers is therefore a very efficient way of increasing the sensibility of next generations to environmental challenges. Since 2015, the national structure called *Maison pour la Science* (MPLS) develops various training programs for teachers in multiple disciplines involving experts (mostly researchers) offering thereby an excellent platform for scientists to target the youngest. Since few years, I am a trainer in two different programs developed by the MPLS: (i) the program *Water: from the Loire river to the laboratory*, and (ii) the program *Biodiversity: from the field to the laboratory and classroom*. I serve as biodiversity expert in these two programs (2 days per year for each program) with about 20-25 participants (teachers at various levels and from diverse disciplines) every time. In these two programs, my aim is to show the extent to which and why dragonfly diversity is important and sensitive to environmental modifications. Dragonflies are a nice model system to explain these issues because they are good-looking; everyone knows what is a dragonfly; and their position in the food web is central (keystone species). During these sessions, I communicate a lot with the teachers about what is feasible or not to

teach kids on biodiversity, creating a sort of feedback loop between what I think is important to tell kids and what is possible to do.

*c) Diffusing science to a broad audience*

As a complement to my teaching and training activities, I try to diversify the channels through which I can diffuse science to an audience as large as possible. My objective is to have 1-2 key actions per year, depending on the opportunities. Such key actions include the publication of an article on the influence of temperature on insects in a vulgarization journal (*Microscop*, edited by the CNRS in our region and read mainly by people already more or less involved in science), my contribution as an expert on biodiversity to a debate-conference on global change during the COP21 event, the participation to the *train du climat* (climate train) event with a stand on climate change and insects while the train stopped in Tours, an oral communication (plenary) on *climate change and insects are both in my garden* during the yearly event *la fête de la science*, and the animation of a short workshop on the biology of dragonflies open for everyone of any age.

## *Part II.*

### Overview of the field: The biology of microclimates

*This section provides an overview of the main concepts used in my research and of the literature on microclimates.*



Russian (ectothermic) dolls — what is the microclimate of these mites on the back of a stick insect standing on plants in Borneo? Maybe not so obvious. Photo: Sylvain Pincebourde.

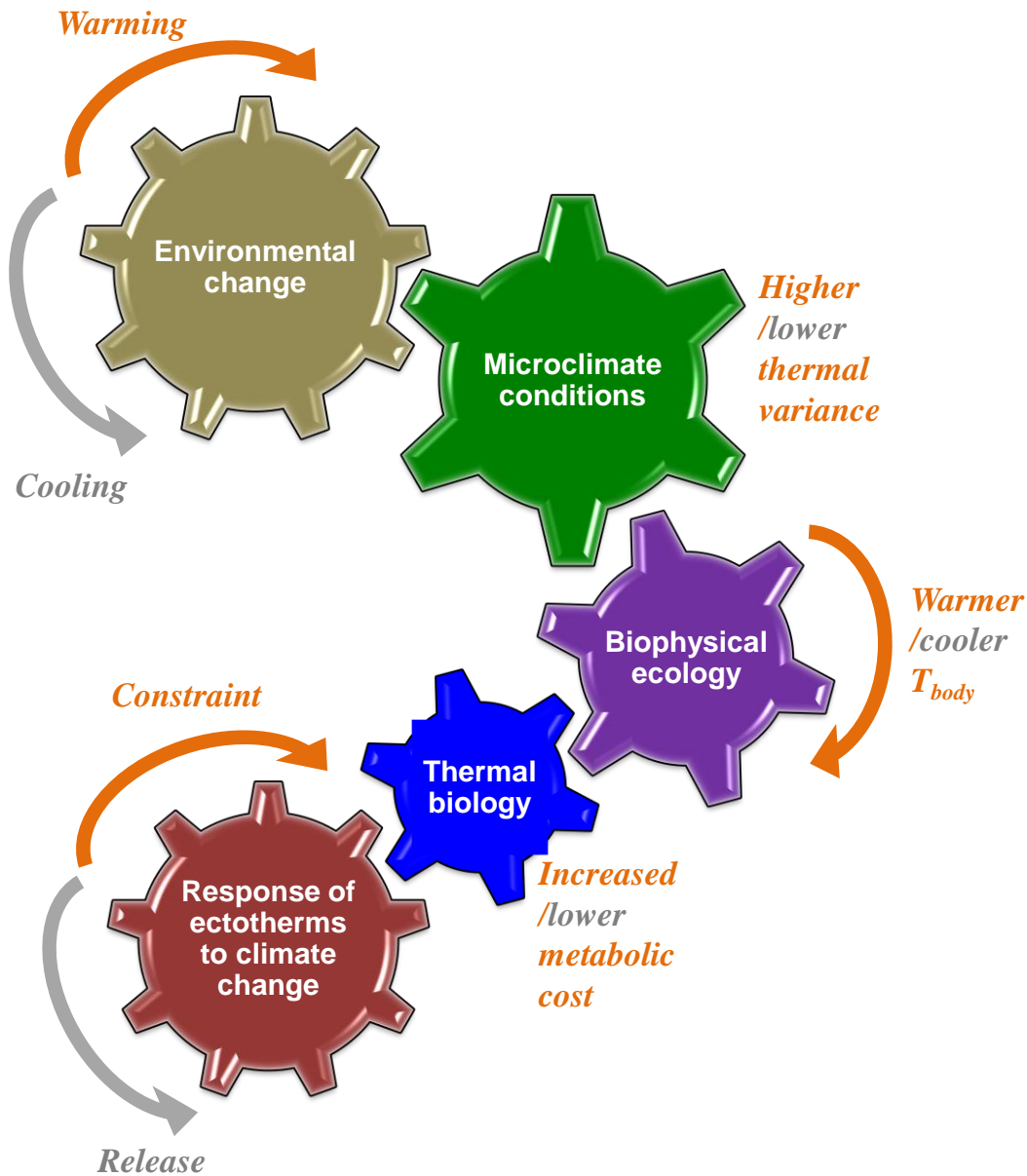
*{ PREAMBLE }*

This section is more my personal view of the literature of interest than an exhaustive synthesis of existing knowledge on the topic. The objective is to provide enough scientific background and context to travel easily across the next section on my scientific production (*Part III*) and to serve as a focal point to assess the novelty and importance of my own work. This section differs clearly from a classical review of the field because it does not intend to provide an exhaustive view of the topics. Instead, I selected specifically the studies that need to be detailed to better understand the fundamental questions I had in mind during my research. I personalize this overview of the field with my own thinking and criticism of some of the selected works.

This dissertation deals with the biophysical ecology of ectotherms and the role of microclimates in their response to environmental changes. I focus on ectotherms (including plants) as these organisms are central to my research but most of the principles detailed in this section also applied to endotherms. Therefore, in this section, I successively explain (Figure II.1):

- (i) What are the environmental changes that matter for ectotherms, in particular in the **context of global change**?
- (ii) Which responses we are expecting to observe. It will be obvious in this dissertation that my research mainly focuses on the responses to high temperatures. A section is then focusing on the **thermal biology** of ectotherms.
- (iii) What are the principles of **biophysical ecology** that allow us to interconnect the ecophysiological responses of ectotherms and the environmental changes?
- (iv) What is known about the **microclimate** of ectotherms and its importance for the future of ectotherms in a changing world?





**Figure II.1.** Schematic illustrating the general approach of this section about how to tackle the response of ectotherms to climate change. Environmental change (e.g., warming) causes changes in the microclimate of species (e.g., higher thermal variance exposing individuals to extremes more often) which lead to warmer body temperatures on average. This translates into a physiological response involving thermal traits (e.g., higher metabolic rate increasing the cost of living). Ultimately, these cascading changes across spatial and functional scales generate the response to environmental change, which constrains ectotherms during warming (or releases them during cooling).

## 1. The global change biology context

Global changes are accelerating now. This section intends to highlight some of these changes that will matter most for the biophysical ecology of ectotherms. Warming rates and their spatial distribution are important aspects that need to be reviewed. A comprehensive view of how the main climate variables shift with time is important to better integrate ecophysiological and macroecological approaches.

### *a) The world is changing faster than ever*

There is no debate now that the earth climate is changing due to both natural and anthropogenic forcing (IPCC, 2014). The fifth Assessment Report of the IPCC (AR5) clearly highlights that the rate of increase in global temperature is accelerating since the second half of the 20th century. The rate of global temperature increase slowed down a little bit however during the period 2000-2012 even if this period gets the record of the warmest decade (Trenberth et al. 2014). The current decade 2010-2020 already surpasses this record by far mostly due to the huge change in global mean temperature in 2015 and 2016 — temperature anomaly almost  $+0.5^{\circ}\text{C}$  in one year (Knutson et al. 2018). The slowdown of global warming in the first decade of 21st century is explained by strong modification in patterns and intensity of large scale phenomenon such as the Pacific Decadal Oscillation (PDO) which generated a deficit in precipitation in some geographic areas (Trenberth et al. 2014). It is not clear, however, how the rate of global temperature change responded after this perturbation left.

The trend of mean global temperature is an important index for atmospheric scientists (and mankind) as this single value can be used to illustrate the climate change underway. Nevertheless, the spatial distribution of this temperature anomaly is at least as much important than the global trend itself. For example, continents are not all warming at the same rate, the Northern hemisphere is warming faster than the Southern side of Earth, and land is warming faster than oceans (IPCC 2014). Most Europe for example will experience higher warming than the global average with important discrepancies across this continent (Vautard et al. 2014). Beyond these geographic differences, the pattern of temperature distribution in space and time is also changing. The spatial autocorrelation structure of temperature is changing

dramatically (Di Cecco & Gouhier 2018): the distance at which temperature become decorrelated is increasing at a faster rate in the tropics than in temperate regions. In addition, this spatial homogenization seems to be accompanied by a temporal homogenization of temperatures across the world. There is a stronger change in daily cycling temperatures (night versus day differences) than in the annual temperature cycling (seasonal differences) at boreal and temperate latitudes while the cycling of tropical temperatures do not change annually and only slightly daily (Wang & Dillon 2014). Here the authors imply that the world is 'flattening' as temperate and polar regions converge toward tropical temperature cycling profiles. Overall, these studies suggest that climate change is leading to the thermal homogenization of the world with great negative impact on the possibility to rescue animal and plant communities. I recall that this homogenization shown by these authors applies to *atmospheric* temperature and not necessarily to *microclimatic* temperatures.

Climate change is more than a change in the mean of climatic variables. The occurrence of extreme events such as heat waves is also increasing at an important rate. The dramatic heat wave we had in Europe in 2003 marked a threshold in the recent history of our climate: since then, the likelihood of exceeding the threshold has sharply increased and the return time of a summer as hot as 2003 is expected to decrease (Christidis et al. 2015). The interaction between climate trends and these extreme events is causing catastrophic biological responses including population collapses and irreversible shifts in ecosystem states (Harris et al. 2018). Even worse, compound extreme events (e.g., heat wave and flash drought) remain poorly explored but are expected to be more devastating, due to their manifold impacts (Chen et al. 2018). Earth system models that simulate biogeochemical cycles and the atmosphere-biosphere interactions are more sophisticated than ever, making possible to develop a mechanistic understanding of how extreme heat waves affect biological processes, ecosystem functioning and adaptation possibilities (Ummenhofer & Meehl 2017). Various indices have been proposed to characterize extreme events that are rare by definition and thus difficult to study. Now these indices are more and more applied by ecologists to study the biological impacts of extreme events (Buckley & Huey 2016; Kingsolver & Buckley 2017).

Climate change corresponds to a change in temperature and precipitation patterns and this is accompanied with many other changes. Recently, a change was noticed in the trend of cloud cover at a global scale (Norris et al. 2016). Observed



and simulated cloud change patterns confirmed the poleward retreat of mid-latitude storms, the expansion of subtropical dry zones, and that the altitude limit of the highest clouds will increase at all latitudes. This is not good news for Earth climate: clouds influence largely the Earth's energy budget by reflecting solar radiation and by limiting the energy loss via emission of thermal radiation into space. Nevertheless, much remains to be done in cloud change research. It is unclear at the moment if the cloud cover will increase or decrease overall, for example (Norris et al. 2016). But a global redistribution of clouds clearly is happening.

Climate change is often associated with the word *global*. Global Climate Models (GCMs) developed by atmospheric scientists operate at a rather coarse spatial scale. Efforts are invested now into the development of Regional Climate Models (RCMs) which provide better predictions for policy makers and researchers that mostly work at the regional scale for conservation biology programs or sustainable agriculture. Initially, RCMs were mostly designed by downscaling statistically from GCMs. The predictive power of RCMs, however, is greatly improved when using a mechanistic approach which consists in understanding the processes underlying the climate signature of a particular region (Hazeleger et al. 2015; Xie et al. 2015). Interestingly, the level of confidence of RCMs' predictions is higher for tropical areas than at temperate and boreal latitudes, mostly because atmospheric variability in the tropics is small relative to the change induced by anthropogenic forcing (Xie et al. 2015). Tropical and sub-tropical localities could become the first zones for which a complete mechanistic downscaling from GCMs to RCMs and local microclimates may be achieved someday. We will see below (section on microclimates) that atmospheric scientists are downscaling and ecologists are upscaling with their microclimate models, but they have not really met just yet: the black hole is now at the local scale, or the scale of the landscape.

*b) Global change biology: from macroecology to ecophysiology*

Although climate change includes a large diversity of shifting variables, most studies looking at the biological impacts of climate change focused mostly on temperature. Indeed, most biological changes mirrored temperature shifts at biogeographical scale. Then, shifting temperature induced various changes at the scale of the organism (genetics, physiology, and morphology), the population (its dynamics and phenology), the species (its geographic distribution) and the

community (biotic interaction strength) (Scheffers et al. 2016). Studies spanning large geographical extents are often quite powerful (and necessary) to relate climate change and species responses despite they mostly rely on correlative approaches. Thus, climate change responses measured at the macroecological level often are difficult to explain mechanistically because we miss the physiological resolution. A typical example is provided by Sunday et al. (2012). Based on the thermal limits of ectotherms, these authors report that terrestrial ectotherms are *underfilling* their thermal niche at the warm boundary of their geographic distribution (i.e., their southern distribution limit is not set by their tolerance). By contrast, they tend to *overflow* their thermal niche at the cold boundary (i.e., their Northern limit is much further North than expected from their thermal tolerance limit). While this and several other papers discuss the potential ecological (e.g. biotic interactions) and physiological (e.g. metabolic rate) processes involved in such spatial mismatch between predicted species distribution based on thermal limits and actual distributions, much remains to be done to comprehend the extent to which physiological traits drive macroecological processes.

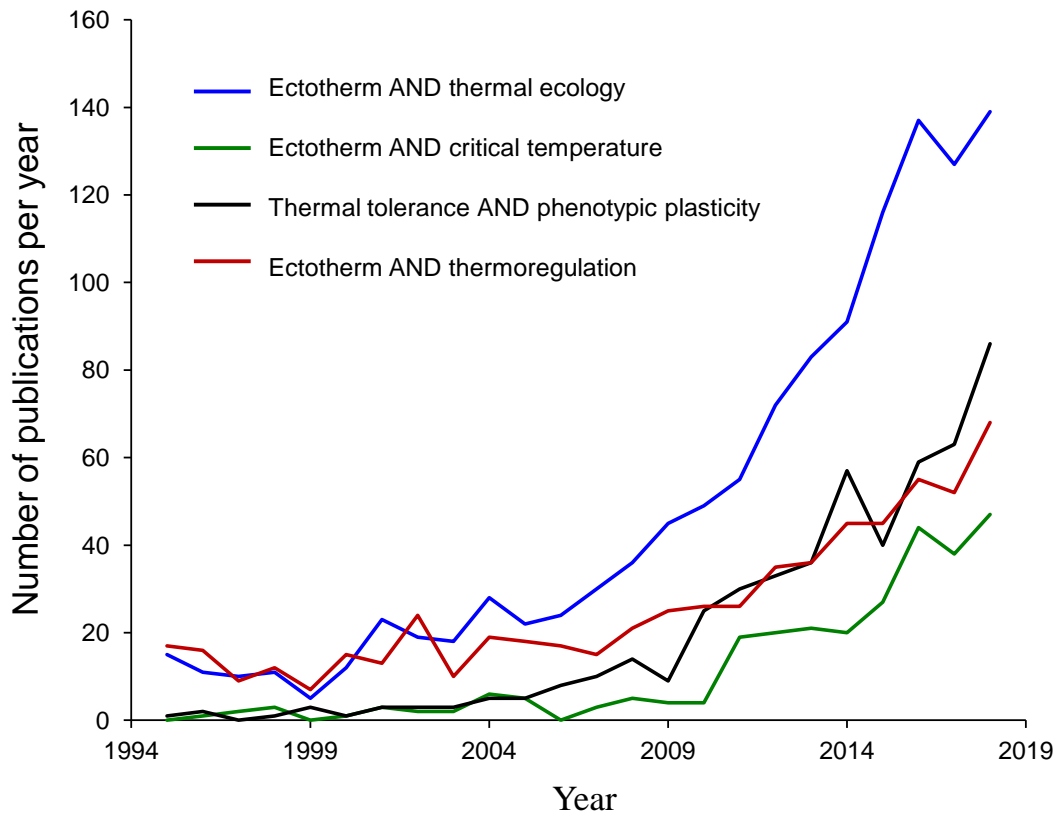
Following the awareness of global changes and the explosion of macroecological approaches to reveal their ecological impacts, the field of macrophysiology has naturally emerged about 20 years ago (Chown et al. 2004). Macrophysiology is defined as the investigation of variation in physiological traits over large geographic and temporal scales and the ecological implications of this variation (Chown & Gaston 2016). Several macrophysiological studies became quite influential, showing thereby the great power of the macrophysiological approach. The most famous example is the development of a database on thermal limits for terrestrial and marine ectotherms (from Addo-Bediako et al. 2000 to Bennett et al. 2018). This database allowed the analysis of thermal limit variations with latitude (Sunday et al. 2011, 2012) including the consequences for thermal safety margin changes across geographical extents (Deutsch et al. 2008; Sunday et al. 2014; Pinsky et al. 2019). Despite an intense debate among physiologists as they are concerned about the use of thermal limit values by macroecologists (see below), this set of studies revealed (i) strong discrepancies between marine and terrestrial ectotherms in their vulnerability to climate warming, (ii) large variations in this vulnerability across latitudes, (iii) and a different macroecological pattern between cold and heat tolerance. In addition, the power of macrophysiology to predict the biological

consequences of the latitudinal gradient of the amplitude of climate warming was nicely illustrated by Dillon et al. (2010). Here, the amplitude of atmospheric warming and the non linear relationship between metabolic rate (of ectotherms) and temperature were integrated in a single framework to reveal that the lowest amplitude of warming in the tropics will produce the highest amplitude of metabolic rate change in tropical ectotherms. Nonetheless, all these studies are based on climatic variables taken at a large spatial scale. Among the 10 challenges for macrophysiology, Chown & Gaston (2016) include the extent to which accounting for microclimate might alter previous macroecological conclusions.

*c) Is climate change making the field of thermal ecology hot?*

On a short note, the field of thermal ecology is rising at a singular rate since about 10 years. Searches on ISI Web of Knowledge using keywords that are central to the field indicate a clear threshold in the period 2009-2011 (Figure II.2). For example, the number of publications on the thermal ecology of ectotherms increased from 30 in 2008 up to a plateau at about 130 publications per year since 2016. The number of publications on the thermoregulation of ectotherms in 2018 is more than two-fold the number in 2009, despite studies on ectotherm thermoregulation became 'classic' in the 80s and 90s following the inputs from authors such as Warren Porter, Raymond Huey, George Bakken, David Gates, James Edward Heath or James Spotila. A similar increasing trend can be seen when using other keywords (Figure II.2). A first explanation to this increase in publication number is that the field of thermal ecology follows the global rate of publications per year (+11% every year; Van Noorden 2014). This global increase, however, started in the 80s and numerous scientific fields display a similar increase starting in the 80s, well before the trend we observe for thermal ecology (a start in ~2009). Another plausible explanation is that the awareness of climate warming stimulated the scientists to explore the ecological consequences of climate change and the extent with which animals can adapt to the changing conditions. Indeed, the Assessment Report 4 of the IPCC was delivered in 2007 and in the same year, the panel received the Nobel Peace Prize. We can speculate that the Nobel Prize finally contributed to give credit to the IPCC. Nevertheless, we cannot exclude that the field of thermal biology suddenly was boosted by the publication in 2009 of the book *Thermal Adaptation: A Theoretical*

and *Empirical Synthesis* by Michael J. Angilletta Jr. This book has received more than 2,000 cites (source Google Scholar). The two hypotheses are not mutually exclusive.



**Figure II.2.** Publication metrics illustrating the rise of thermal ecology in general since about 2009. The number of publications every year (until 2018) was searched using the keywords given in the legend via ISI Web of Knowledge. The data before year 1995 are available but in all cases the trends are lower than the number of publications in years 2000s.

## 2. Principles of thermal ecology

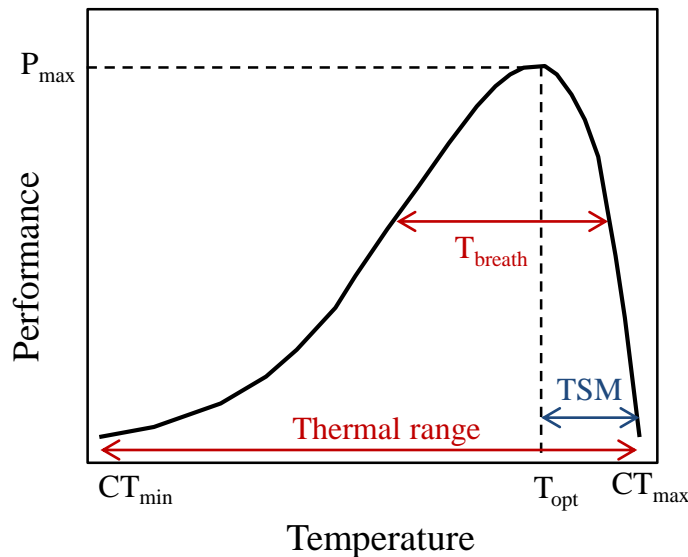
This dissertation mostly focuses on the relationship between temperature and biological/ecological responses. Temperature directly influences physiological rates as it drives enzymatic rates, protein configuration and the stability of the phospholipidic membranes of cells (Somero 1995; Hochachka & Somero 2002). Other abiotic variables matter for life, of course, as we will see later in this dissertation (oxygen, wind speed, solar radiation and so on). Indeed, temperature

interacts with these other variables as some of them are key factors in the heat budget of organisms (e.g., wind speed, solar radiation) while others are physically linked in mass transfer equations (e.g., dissolved oxygen depends on temperature in aquatic systems). Therefore, the central position of temperature for living organisms is reinforced by these multifactorial links. The influence of temperature on a biological trait is best described by Thermal Performance Curves (TPCs) which are reaction norms of biological traits as function of temperature (Angilletta 2009). These TPCs are an excellent start to explain the concepts of thermal ecology that are important in the context of this dissertation: the thermal limits of ectotherms, the plasticity of thermal traits and the influence of behavioral thermoregulation. Note that I use the term of thermal *ecology* and not the usual term of thermal *biology*. Thermal ecology integrates whole-organism and ecologically relevant physiological systems (Huey & Stevenson 1979). While the thermal biologist focuses on how temperature drives physiological processes at the individual, tissue and cell levels, the thermal ecologist attempts to relate the temperature patterns in the natural environment to ecophysiological responses at the individual level. Obviously, the best is to combine both (see Kingsolver 2009).

*a) The Thermal Performance Curve of ectotherms*

TPCs are mathematical expressions of the influence of temperature on a performance trait (Huey & Kingsolver 1989). These curves were measured for a large diversity of performance traits in ectotherms including rates of feeding and digesting, the developmental/growth rate, locomotion or sprint speed, photosynthesis, fecundity, and survival rate that has a particular shape with maximal performance (survival) over a large temperature range (reviewed in both Chown & Nicolson 2004; Angilletta 2009). Several features in this function are important (Figure. II.3). The temperature range allowing the performance is bounded by the critical temperatures ( $CT_{\min}$  and  $CT_{\max}$ ). Within this range, the performance curve is non-linear and often asymmetric. At low temperature, the performance trait increases slowly with a positive first derivative (i.e., the rate of increase is accelerating with temperature) until the inflection point at which the first derivative becomes negative (i.e., the rate of increase is decelerating with temperature). Around this inflexion point, the function can be mostly linear. Indeed, linear functions were used to describe the temperature-dependency of the developmental rate of insects for a long

time, leading to aberrant extrapolations of these linear TPCs outside the temperature range within which they were measured (see Kocourek et al. 1994 for a typical agronomic example). Note that this quasi-linear portion of the curve defines the temperature range within which the degree-day approach can be safely applied (Sharpe & DeMichele 1977; Bonhomme 2000).



**Figure II.3.** Schematic representation of a Thermal Performance Curve relating performance to temperature. The main features are indicated: maximal performance level ( $P_{max}$ ) at the optimal temperature ( $T_{opt}$ ), the critical limits ( $CT_{min}$  and  $CT_{max}$ ), and the thermal range leading to a certain percentage of maximal performance ( $T_{breath}$ , here at about 60%). The thermal safety margin (TSM) is shown as the temperature range between  $T_{opt}$  and  $CT_{max}$ . Redrawn from Sinclair et al. 2016 and Angilletta 2009.

Then, maximal performance is reached at the optimal temperature (Figure II.3). With increasing temperature, the performance drops down at a fast rate such that  $T_{opt}$  is often close to the  $CT_{max}$ . The first derivative of the function is negative and large between  $T_{opt}$  and  $CT_{max}$ : this means that  $+3^{\circ}C$  from  $T_{opt}$  depresses strongly the performance while  $-3^{\circ}C$  from  $T_{opt}$  lowers performance much less dramatically. Such effects related to the influence of skewness of the curve and variance in temperature fall in the concept of the inequality of Jensen (Ruel & Ayres 1999; Denny 2017). This rule states that the response of a system to average (constant) conditions is different from the system's average response to variable conditions (rule also termed

‘the fallacy of the average’; Dillon & Wang 2010; Denny 2017). The effect on a biological performance of this Jensen’s inequality is positive when the function is concave upward (positive first derivative; e.g., metabolic rate as function of temperature) and negative when the curve is concave downward (negative first derivative). The negative consequence on performance is strong when thermal variance increases around the mean temperature centered on  $T_{opt}$ . Combined with the fact that the temperature range between  $T_{opt}$  and  $CT_{max}$  (also called Thermal Safety Margin, TSM, Sunday et al. 2014; also called ‘warming tolerance’, Deutsch et al. 2008) can be as small as few degrees, Martin & Huey (2008) determined theoretically and experimentally that ‘suboptimal is optimal’ (also called ‘risk-avoidance’ hypothesis, Sinclair et al. 2016). That is, the preferred temperature should be slightly lower than  $T_{opt}$  instead of matching it, to increase the TSM without compromising too much the performance.

The use of these TPCs in ecological and global change biology studies was criticized; both about *what* the TPC does not include and about *how* the TPC is applied to particular problems (see Table 1 in Sinclair et al. 2016 which provides an exhaustive view of the underlying hypotheses of TPCs). TPCs are often applied too broadly leading to misuses of this concept. The shape and the key parameters of TPCs often vary depending on the ontogenic stage of a species, and among different performance traits at the individual level (reviewed in Angilletta 2009 and in Sinclair et al. 2016). In other words, the general performance of a given organism is best described by a set of TPCs rather than a single curve. In addition, TPCs provides a value of performance as function of the temperature at given moment without considering the potential influence of time-dependent phenomenon such as the duration of exposure to a given temperature and the temporal pattern of temperature (including the thermal history). For quite a long time this problem was recognized but never really received propositions to solved it. Recently, Kingsolver & Woods (2016) proposed a simple mathematical model that includes the time-dependency of gene expression and protein production during exposure to stressful and non-lethal temperatures. A key determinant of their model predictions is the timescales of response for mRNA and protein concentration. The model is based on the reasonable assumptions that higher temperatures can induce expression of genes associated with stress, leading to the production of stress proteins, and high levels of these proteins can reduce growth rate. The model correctly captures two empirical patterns for



larval growth rate: first, maximal growth rate and optimal temperature decline with increasing duration of temperature exposure; second, mean growth rates decline with time in diurnally fluctuating temperatures at higher mean temperatures (Kingsolver & Woods 2016). This novel approach remains to be integrated into climate change impact or macrophysiology frameworks.

*b) The thermal limits of ectotherms*

The thermal limit of the TPC is a critical feature in global change biology studies (Bennett et al. 2018). Nevertheless, it appears as much crucial to comprehend how they are measured before engaging these data into broad scale analyses. Here, I emphasize three aspects of thermal limits that impose severe limitations to their global use. First, the typical behavior used to infer the temperature at which the CT<sub>max</sub> is reached (loss of muscular coordination) is often a subjective measure prone to errors and biases. While this behavioral approach yields accurate CT<sub>max</sub> results (e.g., Burton et al. 2018; Oyen & Dillon 2018), it may not be appropriate for tiny arthropods for which the loss of movement cannot be readily observed (DeVries et al. 2016). The technique of thermolimit respirometry is an objective alternative to the behavioral approach as it focuses on the stereotyped release of CO<sub>2</sub> when the spiracular control is lost right after the CT<sub>max</sub> was reached (Lighton & Turner 2004).

Second, the determination of the CT<sub>max</sub> depends on the methodological context. In particular, both the rate of temperature increase and the temperature at which the temperature ramping starts (in a dynamic ramping assay) can profoundly change the endpoint CT<sub>max</sub> (Terblanche et al. 2011). Acclimation temperature can also interact with the rate of increase leading to different CT<sub>max</sub> values (Chown et al. 2009). The interaction between starting temperature and the rate of increase determines the duration of exposure. In general, higher CT<sub>max</sub> values are obtained at higher rates of temperature increase and at shorter experimental durations (Terblanche et al. 2007). Exceptions certainly abound. For example, higher rates of temperature increase produce lower CT<sub>max</sub> in *Ceratitis* flies (Nyamukondiwa & Terblanche 2010). This suggests, however, that fully-factorial designs may be necessary to infer the CT<sub>max</sub> that is the most ecologically-relevant (as in Terblanche et al. 2007). Alternatively, if the microclimatic conditions experienced by the



ectotherm are known, one can design the thermal-ramping assay based on ecologically-relevant conditions (Terblanche et al. 2011).

Third, the CT<sub>max</sub> corresponds to the temperature at which locomotor coordination is lost, and this threshold does not necessarily imply the death of the organism. The temperature inducing directly mortality (Upper Lethal Temperature, ULT) can be 5-10°C higher than the CT<sub>max</sub> in marine Copepods (González 1974) and about 4°C higher in the Argentine ant (Jumbam et al. 2008). Overall, we know little on this range between the CT<sub>max</sub> and the ULT in ectotherms: a comparative study across species living in various thermal environments remains to be done to understand the constraints determining this range. The reasoning behind the CT<sub>max</sub> threshold is that the organism is losing locomotor ability and therefore it should die at some point if the temperature continues to increase. However, the ectotherm is likely to survive if temperature starts to cool down somewhere between the CT<sub>max</sub> and the ULT. Interestingly, this scenario opens up possible strategies for organisms to survive the heat. For example, aphids fall down from their host leaf to the ground when they overheat ('dropping' behavior; Ma & Ma 2012). By doing so, the aphids meet suddenly more favorable (cooler) temperature near the ground compared to the temperature at the surface of wheat leaves in the sun (Ma & Ma 2011). The benefit of such behaviors, in terms of survival and fitness, likely depends on the range between the CT<sub>max</sub> and the ULT.

### *c) Phenotypic plasticity of thermal traits*

The thermal traits at the individual level, such as the parameters identified in the thermal preference curve above, can be plastic. Plastic responses are of interest in the context of climate change because they allow individuals to respond rapidly to environmental changes (by contrast to evolutionary responses that are slower because they involve genetic changes across generations). Several types of phenotypic plasticity were identified, including acclimation (and acclimatization in the natural environment), heat hardening and diapause (Sgrò et al. 2016). For example, higher acclimation temperature promotes survival in invasive springtails while it decreases it in native species, indicating that warming is advantaging invasive species via their higher thermal plasticity (Chown et al. 2007). Another type of plasticity is transgenerational. A plastic response may occur across several generations to cope with rapid climate change, but it is often difficult to separate

from within-generation plasticity (Donelson et al. 2018). Trans- and within-generational plasticity may however be related to different time scales of environmental changes. While developmental plasticity of individuals (within-generation) could be more influenced by acute extreme events or stochastic weather fluctuations (Burggren 2018), the trans-generational plasticity can be associated to the amplitude of long term changes and to the timing of acute events relative to crucial reproduction stages (Donelson et al. 2018).

The *temperature-size rule* is one of the most documented forms of phenotypic plasticity as it occurs in nearly 80% of ectotherms (Atkinson 1994). Body size affects nearly all aspects of an organism's morphology, physiology, performance, and therefore fitness. Body size also influences body temperature in ectotherms (Stevenson 1985). The temperature-size rule proposes that higher temperatures during development result in smaller adult body size (Kingsolver 2009). This rule was confirmed for most ectotherms. Several mechanisms explain this fundamental relationship, including an endocrine signal that stops growth at lower critical size under higher temperatures (Ghosh et al. 2013), the co-influence of elevated temperature on faster growth but over a shorter period (Davidowitz & Nijhout 2004), or resource limitation at elevated temperature impeding reaching large body size (Hoefnagel et al. 2018). This rule may be reversed in some species by environmental factor such as the shift to a low-quality host plant in herbivore insects (Diamond & Kingsolver 2010). Globally, this rule illustrates well the complexity of the interactive effects between physiological variables and environmental factors on a traits linked to temperature (see Kingsolver 2009).

Given the potentially large flexibility of thermal traits, the extent to which thermal phenotypic plasticity can buffer environmental changes was the focus of intense research this past decade in particular. Several studies reported that the scope for plasticity to increase upper thermal limits was rather limited compared to the amplitude of climatic change in terrestrial organisms. For example, plastic responses to acclimation and/or developmental temperature increased the upper thermal limit by up to  $\sim 1^{\circ}\text{C}$  in *Drosophila* (van Heerwaarden et al. 2016). In addition, the level of phenotypic plasticity is at best weakly related to the geographic distribution of *Drosophila*, with slightly lower plasticity in tropical populations, suggesting again a low potential for upper thermal limit plasticity to buffer against thermal stress (Mitchell et al. 2011). A similar shift in upper thermal limit was observed in the

caterpillar of *Manduca sexta*: acclimation via repeated exposure to acute/chronic high temperatures resulted in an increase of  $\sim 1.5^{\circ}\text{C}$  of the CTmax (Kingsolver et al. 2016). Although this plastic response was modest, authors proposed that a  $1\text{-}2^{\circ}\text{C}$  shift could already improve survival since this species can frequently meet challenging temperatures in the desert environment.

This plastic increase in upper thermal limit during acclimation is not quite reversible such that developmental temperature constrains heat tolerance of later stages (Slotsbo et al. 2016). Such carry-over effects of early thermal history across ontogeny are relatively frequent in insects and gastropods for example (Potter et al. 2011; Klockmann et al. 2017). This carry-over effect can be combined with genetically fixed differences in thermal tolerance among different life stages in ectotherms with complex life cycles (Bowler & Terblanche 2008; Truebano et al. 2018). In addition, environmentally driven developmental plasticity in thermal tolerance can be inversely related to growth in juveniles, as shown recently in the rocky intertidal mussel *Mytilus californianus* (Gleason et al. 2018). Indeed, both genetics and thermal history contribute to thermal tolerance but the plasticity observed in juvenile mussels was not observed in adults. Therefore, the plasticity of thermal traits at all stages should be assessed to detect the ‘weakest link’ of ectotherms’ life cycle (Pandori & Sorte 2019).

Aquatic ectotherms usually show a greater ability to buffer environmental extremes via plastic responses in their thermal traits compared to terrestrial ectotherms. For example, acclimation to warmer temperature induced a shift of  $\sim 4^{\circ}\text{C}$  in both CTmax and Topt in a frog species (Ruiz-Aravena et al. 2014) and of  $\sim 6^{\circ}\text{C}$  in the CTmax of a killifish species (Healy & Schulte 2012). Exceptions exist such as marine copepods in which developmental acclimation allows to increase thermal tolerance by no more than  $1.3^{\circ}\text{C}$ , a value similar to terrestrial ectotherms (Pereira et al. 2017). In general, the slope of the line describing the change in thermal tolerance with a given change in acclimation temperature is about 3-fold higher for fishes and crustaceans (value  $0.3^{\circ}\text{C}$  increase in CTmax per  $1^{\circ}\text{C}$  increase in environmental temperature) compared to insects and reptiles ( $\sim 0.1^{\circ}\text{C}/^{\circ}\text{C}$ ) (Gunderson & Stillman 2015). Beyond the specific thermal traits of the TPC, its non-linear shape can also be influenced by acclimation. A global analysis of physiological rates and their sensitivity to temperature changes among terrestrial, freshwater and terrestrial ectotherms showed that (i) acclimation capacity was greater in species living in more

stable thermal environments (i.e., marine and freshwater), and (ii) acclimation decreases the sensitivity of physiological rates to warming especially in marine and freshwater organisms (Seebacher et al. 2014). This study judiciously integrated the van't Hoff's equation (Q10) and the effect of acclimation on the TPC for physiological rates to provide the most realistic physiological estimate of ectotherms' sensitivity to long-term temperature changes.

Plastic responses (beyond TPCs and the direct effect of temperature on development of insects for example) remain to be included into models to forecast the impacts of climate change on the thermal safety margin and vulnerability of ectotherms (Sgrò et al. 2016; but see Valladares et al. 2014 for an example of such integration to model tree species distributions depending on their plasticity). Short-term mechanisms such acclimation and heat hardening are difficult to integrate into models that run with long temporal steps. Again, models considering the time-dependency of gene expression and protein production (Kingsolver & Woods 2016) will certainly provide a key for mechanistic models to incorporate plasticity in thermal traits into models of global change impacts. The processes discussed above are deterministic but stochastic physiological noise may also produce plasticity (Woods 2014), although its potential influence on climate change responses remains virtually unexplored.

#### *d) Thermoregulation in heterogeneous environments*

In ectotherms, another mean to buffer against environmental changes is to modulate body temperature. Thermoregulation involves a long list of possible mechanisms in ectotherms, and my purpose here is not to review all of them. In general, **behavioral mechanisms** (changing microhabitat, posture relative to the sun etc.) allow a four to five times higher amplitude of change in body temperature than physiological processes (modulating evapotranspiration, cardiovascular adjustments etc.) (Stevenson 1985). Therefore, behavioral thermoregulation has received most of the attention in the context of global change biology. In particular, one crucial question is to what extent behavioral thermoregulation can help ectotherms to buffer the amplitude of warming. *A priori* simple question but complex answer.

One of the most influential studies that attempted to answer this question with a global, mechanistic approach indicated three important aspects (Kearney et al.

2009). First, climate warming will induce changes in both daily and seasonal activity patterns in ectotherms such as reptiles. While warming will extend the activity period during winter mostly at temperate latitudes, it will also restrict considerably the daily activity in tropical and continental areas to avoid overheating in the middle of the day. Second, the availability of shade (e.g. under vegetation) is a key factor for behavioral thermoregulation. Only moderate levels of shade are required for thermoregulation at temperate sites but deep shade is needed at the continental and tropical sites to maintain the same daily and seasonal patterns of activity under climate warming. Third, there is a mismatch between the required and the available amount of shade globally such that some regions do not harbor the vegetation required to provide enough shade for efficient behavioral thermoregulation, while other regions may have too much shade. Indeed, warming-induced restricted activity period does not fully explain some of the recent extinctions in lizard populations. Instead, the loss of shade (i.e., the decrease in vegetation cover due to warmer and drier climates) is the most likely explanation for these extinctions (Kearney 2013). More generally, the availability of refuges with favorable conditions for a generic ectotherm to escape the heat during the warmest portions of the day/month/season is a key factor for most lizards, insects and dry-skinned amphibians not only in the tropics but also at temperate latitudes (Sunday et al. 2014). Beyond the amount of shade available, the spatial configuration of these favorable refuges matter too for behaviorally thermoregulating ectotherms. Lizards thermoregulate more accurately when thermal patches are dispersed throughout space than when they are clumped (Sears et al. 2016). Testing the role of behavioral thermoregulation to buffer warming amplitude therefore requires integrating behavior, habitat structure and environmental variables, and their dynamics across various spatial and temporal scales (Huey et al. 2012).

In the context of global warming, there is concern that behavioral thermoregulation may inhibit plastic physiological responses, thereby limiting the possibility for acclimatization and further for adaptation to climatic changes. Bogert (1949) was the first to argue that regulatory behaviors might eliminate environmental changes such that little or no selection for physiological change would apply. This ‘behavioral inertia’ has been termed the ‘Bogert effect’ (see Marais & Chown 2008). In the context of phenotypic plasticity, it is clear that behavior might likewise act to minimize the extent of environmental variability experienced by an ectotherm,

thereby reducing or perhaps eliminating any selection for plastic and acclimation responses. In other words, in response to a warmer temperature, an organism could simply seek out a cooler microclimate, rather than alter its physiology to perform better in the new environment. There is concern, therefore, that although behavioral plasticity is beneficial in the short-term, it will ultimately limit the physiological adaptation necessary to endure future warming (Buckley et al. 2015).

Several thermal traits are necessarily integrated with each other to assess the efficiency of ectotherm thermoregulation, including field body temperatures, optimal temperature, operative temperatures available and preferred temperature range (Angilletta 2009). Among these traits, the preferred temperature range is of particular interest because a maladapted preferred temperature can produce high vulnerability to environmental change even if the other traits match well the new conditions. The preferred temperature range has been mostly measured in reptiles (Clusella-Trullas & Chown 2014) and fishes (Reiser et al. 2013), and to a lesser extent on insects (Kay 1978). The measurement of the preferred temperature range is not as simple as it seems *a priori* because several confounding factors may jeopardize the estimate including the effect of temperature on locomotion or starvation while the ectotherm is in a thermal gradient (Angilletta 2009; Dillon et al. 2012). Nevertheless, the preferred temperature range of ectotherms seems to be particularly plastic to abiotic and biotic changes (Smolinský & Gvozdík 2012). For example, preferred temperature can shift when food availability is restricted to lower the metabolism and save energy (Gilbert & Miles 2016). Moreover, in warmer environments, directional selection can favor lizards with higher thermal preferences and faster sprint performance at their optimal temperature ('warmer is better'; Gilbert & Miles 2017). Negative correlational selection may also exist between thermal preference and critical thermal maxima, favoring individuals that prefer warmer body temperatures with cooler critical thermal maxima (Gilbert & Miles 2017). This counter-intuitive result is explained by the extent to which warmer environment selects for thermal specialists rather than generalists, and thermal specialists display in general a narrower temperature range with lower CT<sub>max</sub>. Coadaptation between preferred temperature range and the other thermal traits can be tight under some circumstances like when ectotherms already select high temperatures (Huey & Bennett 1987). Overall, the level of plasticity of preferred temperature range, however, is relatively

overlooked in climate change studies compared to other thermal traits (Gvozdík 2012).

Finally, behavioral thermoregulation is also modulated by factors that are not necessarily directly linked to environmental temperature. For example, the concept of thermos-hydroregulation integrates the influence of water status on thermoregulation in lizards such that body temperature and water balance are linked functionally (Rozen-Rechels et al. 2019). In addition, the energy costs of behavioral thermoregulation is associated to the structure of the environment (Sears & Angilletta 2015), and therefore the nutritional status of the animals or their physiological status could interfere on the decisions taken when thermoregulating. Another interesting and overlooked interface is given by the co-influence of solar energy input and body coloration patterns for crypsis on the choice of body orientation. Luckily, the body orientations that allow the optimal use countershading to enhance crypsis can be similar to those that allow optimal solar heat inflow and UV protection (Penacchio et al. 2015). A complete framework integrating all these complexities remain to be developed.

### **3. Principles of biophysical ecology**

David M. Gates (1980) was among the first to formalize the field called biophysical ecology. He defined biophysical ecology as the detailed analysis of the processes happening at the scale of the individual, and of the interactions between organisms, including the physical mechanisms relating the organism to its environment and the biophysical aspects of the physiological reactions. Gates admitted that the term biophysical ecology is necessarily redundant because the study of ecology includes by definition the physics of the environment and the physiological processes. This term, however, best describes the general conceptual approach of this scientific field. Biophysical ecology as I treat it here is thus a sub-domain of physical ecology which includes fluid dynamics (Casas & Dangles 2010) and mechanics (Denny 2016). The field of biophysical ecology applies the principles of thermodynamics to derive mechanistic models of these processes and their physiological consequences (Porter & Gates 1969; Gates 1980). The core of



biophysical ecology consists in determining the different ways of gaining and losing energy for a given organism in a given environment, allowing one to compute the body temperature (for ectotherms) or the amount of energy burnt to maintain body temperature (for endotherms). While this approach can equally be applied to endotherms (e.g., Natori & Porter 2007), I only deal with ectotherms in this section for simplicity. Below, I put emphasis on the two most important aspects of biophysical ecology for my research: (i) the ability to forecast the body temperature of ectotherms and (ii) the identification of the mechanisms that control for body temperature.

*a) The body temperature of ectotherms: an integrative trait*

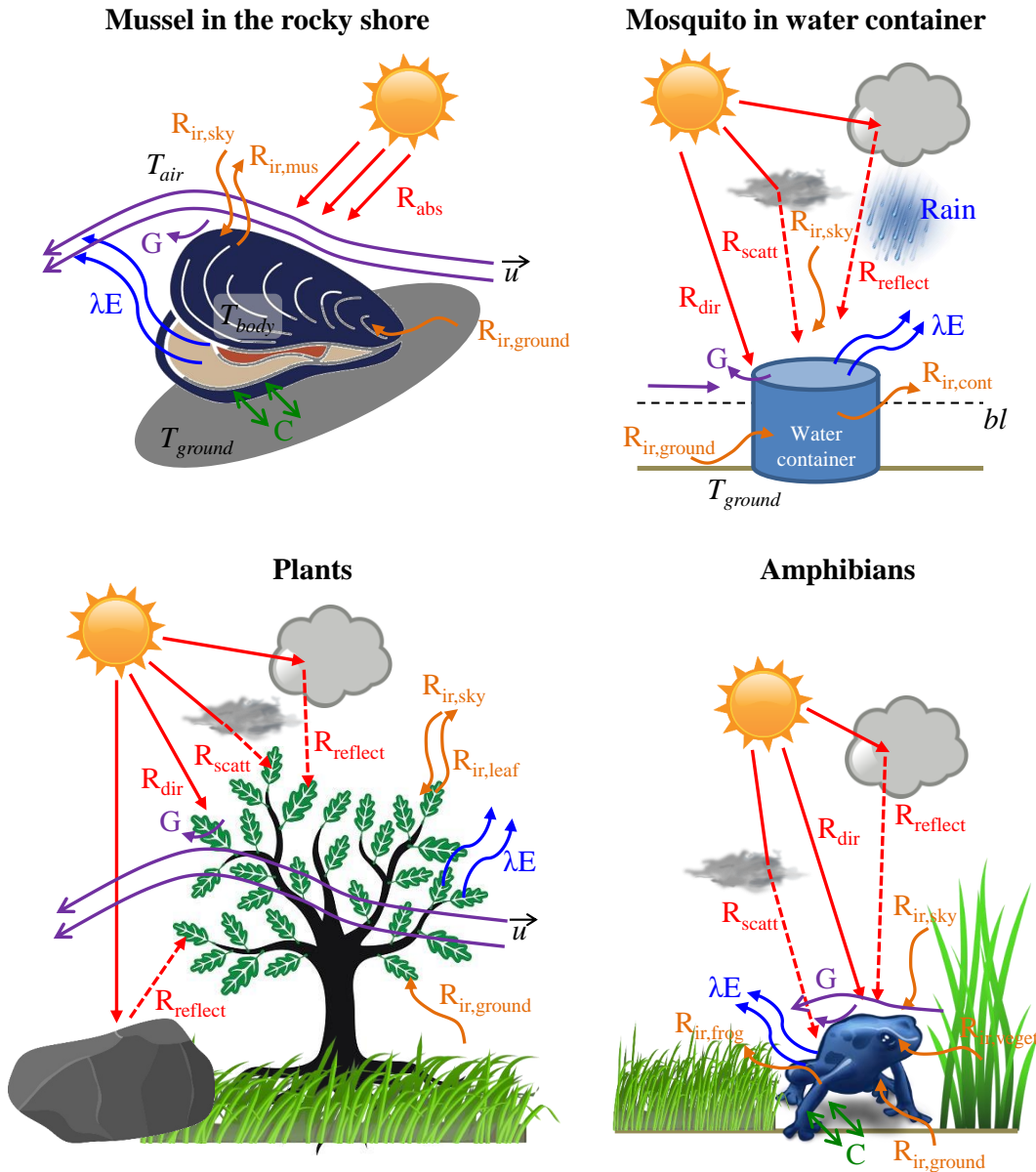
Ectotherms do not produce metabolic heat (except during phases of endothermy for flying insects for example; Heinrich 1987). As a result, most terrestrial ectotherms are also poikilotherms: their body temperature fluctuates depending on the variations in their environment. A too simplistic shortcut that I quite often see in the literature, especially on arthropods (less true on reptiles), is to consider that the body temperature of ectotherms equals ambient air temperature (most of the time meteorological air temperature taken at 2m above ground). The body of literature showing that this is not true most of the (daily) time is now substantial (e.g., Casey 1976; Stevenson 1985; Helmuth 1998; Huey & Pianka 2018).

Instead, the body temperature of an ectotherm is driven by several processes of heat exchange between the body and the micro-environment (Figure II.4). Energy is received by the organism from solar radiations, either directly or indirectly (radiation diffused by clouds, reflected by other elements in the environment etc.). Thermal infrared radiation is also received and emitted by the body depending on the temperature of each element (black body law). Then, energy can be conducted and/or convected between the body and the substrate or the fluid surrounding the body (sensible heat). Finally, energy is lost by the ectotherm during evapotranspiration (latent heat). The heat budget of an ectotherm is a balance: body temperature adjusts according to the environmental conditions until the energy gain equals the energy loss. The relative amounts of convective, evaporative and radiative heat exchange between an ectotherm and its environment depends largely on the level of incident radiation. In general, body temperature excess is high if energy gain is high, and it is low under low radiation level (Gates 1980). Numerous environmental factors



influence biophysical budgets (Helmuth 1998; Campbell & Norman 1998), including solar radiation (direct, diffuse, reflected; Figure II.4), the thermal infrared radiation radiated by the elements of the landscape (other organisms, ground, sky; Figure II.4), air temperature, wind speed, and humidity in its broad definition (the vapor pressure deficit is more informative than relative humidity for biophysical ecologists). Indeed, simple biophysical models can be drawn by neglecting the architecture of the environment and the elements that reflect solar radiation. By contrast, the most complex heat budgets includes the complexity of having multiple sources of solar radiation reflections and thermal infrared re-radiation from all elements in complex architectures like plant canopies (Sinoquet et al. 2001).

Every ectotherm owns a set of traits that is related to the heat budget. These traits serve the organism to filter their proximate environmental conditions, thereby determining its body temperature (the concept of organismal filter; Angilletta 2009). These traits represent the first line of defense of ectotherms when the environment becomes challenging. The body coloration (e.g., the thermal melanism hypothesis) determines the amount of incoming radiative energy that is absorbed by the organism in the visible range (Clusella-Trullas et al. 2008). The geometric traits such as body size, shape and orientation can be adjusted to manipulate the amount of incoming radiative energy acquired (Lathlean et al. 2016). The evapotranspiration strategies developed by the ectotherm directly sets the amount of latent heat loss (Prange 1996). In some ectotherms, metabolic heat production allows to increase body temperature significantly (Heinrich 1996). All these traits are the first candidates when investigating adaption potential to climate warming in ectotherms or the role of phenotypic plasticity to decrease vulnerability to short-term events. For example, the body of European dragonflies and butterflies is becoming lighter (less melanin) at the Southern distribution limits and darker at the Northern limit, with a concordance with the dynamics of temperature increase since the 90s (Zeuss et al. 2014).



**Figure II.4.** Schematic representations of heat exchange between an organism and the environment for a mussel in the rocky shore (redrawn from Helmuth 1998), a water container with mosquito larvae (redrawn from Kearney et al. 2009), a tree in an open field (redrawn from Gates 1968), and a frog (redrawn from Tracy 1976). The fluxes associated with the radiative heat budget are direct solar radiation ( $R_{dir}$ ), solar radiation reflected by clouds of elements in the environment ( $R_{reflect}$ ), scattered solar radiation due to dust or water vapor in the air ( $R_{scatt}$ ), and the thermal infrared radiation emitted proportionally to body temperature by the ground ( $R_{ir,ground}$ ), the atmosphere ( $R_{ir,sky}$ ), the vegetation ( $R_{ir,veget}$ ) and the bodies themselves ( $R_{ir,mus}$ ,  $R_{ir,cont}$ ,  $R_{ir,leaf}$  and  $R_{ir,frog}$ ). The heat exchanged via conduction ( $C$ ) depends on the temperature difference between the body ( $T_{body}$ ) and the surface ( $T_{ground}$ ). Convection processes ( $G$ ) are influenced by wind speed ( $u$ ) and the development of the boundary layer of the surface and body (shown only for the water container,  $bl$ ). The latent heat loss ( $\lambda E$ ) during evapotranspiration is driven by the vapor pressure deficit of the body's surface (and also by rainfall inputs in the case of the water container).

*b) The aim of biophysical ecology: unraveling the mechanisms*

The principles of biophysical ecology have been largely applied in the 60s-80s to determine the links between body temperature and environmental variables (Church 1960; Porter & Gates 1969; Kingsolver & Watt 1983). At that time, the objective was mostly to quantify the energy flows between the ectotherm's body and its proximate environment. For example, Gates (1962) applied a biophysical model of heat exchange between a leaf and its environment to describe the biophysical mechanisms leading to the large temperature excess of leaves in the sun (up to 20°C above ambient air temperature). This study was among the first to really quantify the effect of evapotranspiration on leaf temperature in plants, opening the exciting and still hot topic of plant thermoregulation (Michaletz et al. 2015, 2016). During this period, energy balance models were strongly and firmly based on thermodynamics law of heat and mass transfers, but Warren Porter wrote in 1975 that 'transient energy-balance models were needed and had to include more biology along with physics and engineering. Microhabitat specification was needed. Tests needed to be done on live animals in both controlled environmental facilities and out of doors' (Porter et al. 1975). Climate-space niche models started then to integrate more about the biology and ecology of the ectotherms with climate variables (e.g., Porter et al. 1973). This biophysical, truly mechanistic approach was later applied to flying insects (Rainey 1974) and other insects (Willmer & Unwin 1981), amphibians (Tracy 1976), pitcher plants (Kingsolver 1979), and even on dinosaurs (Haack 1986). All these studies provided quantitative assessments of the influence of particular environmental parameters on the body temperature of ectotherms. For some reasons, biophysical models of ectotherm energy exchanges were much less used from end of 80s to end of 90s. The only reason I can imagine is that during this period most of these authors started to initiate strong developments on the evolutionary ecology of thermal sensitivity in ectotherm performance (Huey & Kingsolver 1989), keeping them busy on something else (although not disconnected!).

From end of the 90s and early 2000s, biophysical ecology started to (re)emerge as a potentially powerful tool to quantify the impact of climate change on the energy budget of ectotherms (Helmuth 1998; Kearney & Porter 2004). In the 90s, Brian Helmuth (1998, 1999) was the first to take up biophysical ecology principles by applying them on mussels in the rocky intertidal to comprehend their heat budget and to what extent they live near their physiological limits while in mussel beds high

on the shore. This study quantified the time dependency of the relationship between mussel body temperature and environmental conditions via its thermal inertia (Helmuth 1998). The understanding of the biophysical mechanisms controlling the body temperature of mussels forged the mechanistic background that later determined the tide cycle-induced geographic mosaic of thermal stress in the Californian mussel in opposition to a classic view of a monotonic increase of body temperature with latitude (Helmuth et al. 2002, 2006). Biophysical models of mussel body temperature allowed to quantify how much of the amplitude of warming will be transferred into the body temperature of mussels, highlighting a high variability in the amplitude of warming-induced body temperature changes (Gilman et al. 2006). Nevertheless, the direct link between biophysical mechanisms controlling for body temperature and the geographic distribution of species, thereby mapping the fundamental niche, was formalized first by Kearney & Porter (2004). In this seminal study, the author combined physiological measurements of a lizard and high-resolution climatic data for the Australian continent with biophysical models to calculate the climate niche space of this lizard and map it onto the Australian landscape for current climate (at that time) and for a global warming scenario.

Thus, this *re-appropriation* of biophysical ecology by ecologists in this global change context (Helmuth et al. 2005) happened concomitantly with the early development and explosive use of climate envelopes of species which formed rapidly the basis for *correlative* species distribution models (Pearson et al. 2002; Pearson & Dawson 2003; Guisan & Thuiller 2005; Araújo & New 2006; Elith & Leathwick 2009; Higgins et al. 2012). Correlative (statistical) versus mechanistic (biophysical) approaches of mapping the fundamental and realized niches of species were often discussed as opponents. The advantage of correlative approaches is that they require less parameters and input data than biophysical models — an advantage for poorly studied taxa. However, the biophysical approach allows to comprehend and explain the processes controlling for species distributions while the statistical method is often blind to the mechanisms at play (Kearney & Porter 2004; Kearney & Porter 2009). In a global change biology context, mechanistic models are certainly more robust and reliable (e.g., by extrapolating using the non-linear relationship between physiological rates and temperature) than correlative species distributions models (which often extrapolate using default relationships, i.e., linear) (Kearney & Porter 2009; Maino et al. 2016). Finally, hybrid models mixing the strengths of both

correlative and mechanistic (or process-based) approaches should generate major progress in species distribution modeling (Dormann et al. 2012). Such hybridization between statistical and deterministic approaches also occurred in the 90s-2000s in the field of population dynamics (Jérôme Casas, personal communication). Nonetheless, mechanistic models are best suited to be implemented into other deterministic models including metabolic theory, nutritional geometrical framework and dynamic energy budgets (Kearney 2012; Kearney et al. 2013; Malishev et al. 2018).

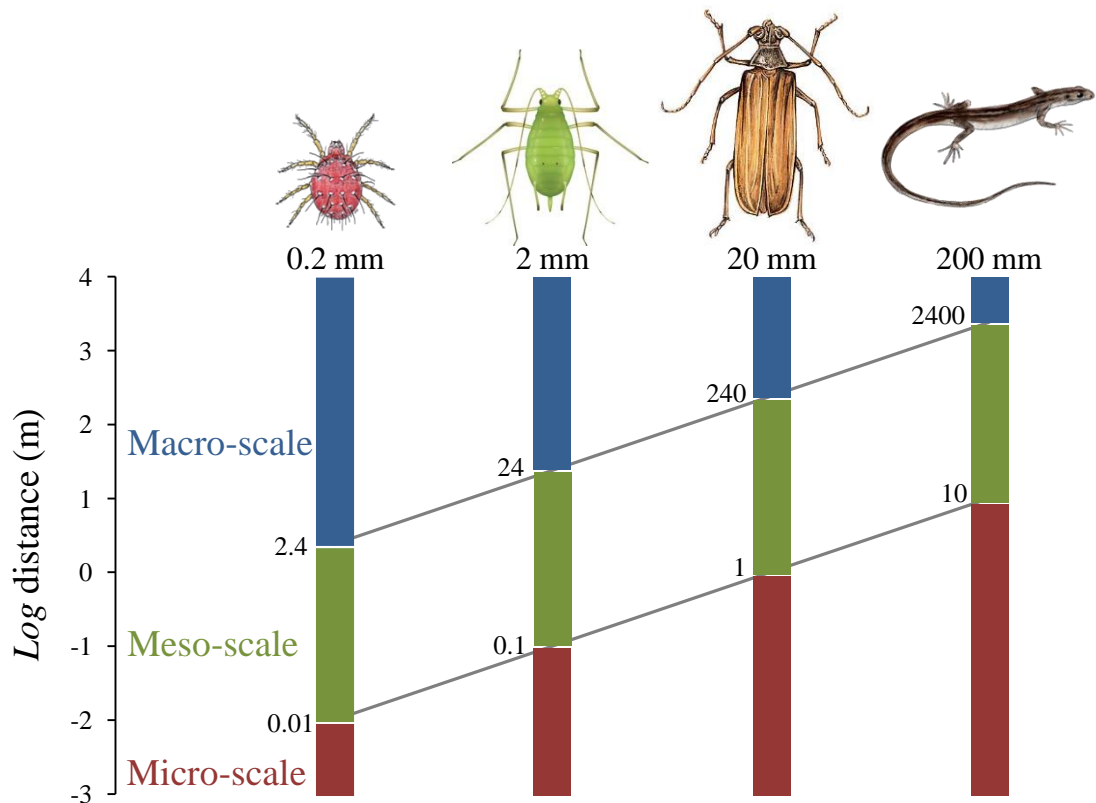
#### 4. The microclimate of ectotherms

The term 'microclimate' is part of our daily vocabulary. While microclimatology is often seen as a sub-discipline belonging to climate research, it was indeed a German botanist who became, according to Rudolf Geiger (Geiger 1959), the father of microclimatology (Gregor Kraus, 1841-1915). Since the beginning, the science of microclimates is inherently a multidisciplinary topic involving ecologists, zoologists, botanists, entomologists, physicians, geographers, and even technicians and tradesman during street or house constructions. As such this field bears various key concepts. Here, I only barely touch upon the main key ideas that microclimatology provides for ecologists interested in the actual temperature experienced by species in their microhabitat: (i) the notion of spatial scaling of microclimates, (ii) which temperature is the right one depending on the studied species, (iii) how do we model microclimates to predict the right temperature, and (iv) what is the impact of climate warming on these microclimates? I finish this section with an extensive description of what was known, before my works, on the leaf microclimate, which is my main biological model.

##### *a) The spatial scale of microclimates*

The microclimate (i.e., climate at microscale) has been defined in slightly different ways depending on the discipline or the context. A quite general, all-purpose definition states that microclimates are fine-scale climate variations that *deviate* from the background atmosphere at least temporarily (Stoutjesdijk & Barkman 2014; Bramer et al. 2018). Note that I use the term 'deviate' instead of the

word 'decoupled' in the original version of this definition (Bramer et al. 2018). The temperature in the forest understory can deviate strongly from atmospheric temperature (De Frenne et al. 2013, 2019), but this deviation does not necessarily imply a full decoupling between the two. For instance, a long, intense heat wave event can still bring the forest understory to extreme temperatures especially during dry periods. The notion of microclimate often includes a spatial extent scale. For example, microclimate corresponds to horizontal distances of 0.001-100 m while mesoclimate lies in the range 1-200 km and macroclimate corresponds to distances >200 km (Bramer et al. 2018). However, this scale is largely biased by our own (Human) vision. A distance of 100 m may not mean the same for an aphid or a large reptile. To quantify this effect, we can calculate the ratio [horizontal distance / body size] corresponding to the transitions from micro- to meso- to macro-climate based on the distance limits given above and assuming the body size of Human as 1.70m. We obtain that mesoclimate starts at a ratio of 50 and macroclimate at 12,000. Then, for any body size we can go back to the horizontal distance corresponding to each scale (Figure II.5). This quite simple approach makes the point that the scale corresponding to macro-climate for a tiny spider mite (e.g., 3m) matches the micro-scale relative to the body size of a lizard (Figure II.5). Indeed, for organisms with very small body size, the term nano-climate was sometimes employed, referring to the climate within surface boundary layers such as a leaf surface or air cavity in the soil (Stoutjesdijk & Barkman 2014). This term was however never really used by ecologists and physiologists, and indeed this term is no longer needed if we scale the micro-scale climate relative to body size (Figure II.5).



**Figure II.5.** Illustration of the distances corresponding to each type of spatially scaled climate for various ectotherms differing in body size. The Y-axis shows the log scale of the distance. The numbers in the graph provide the actual distances (in meters) delimiting the different spatial scales.

*b) Which temperature is the right one?*

Why should we care about microclimates? One answer is: because there is large evidence that the temperature in most microclimates deviate from ambient air temperature. The literature reporting microclimate temperature deviations abounds. Therefore, to remain concise, I spot subjectively to the studies that I personally found quite illustrative. I also make the point in this section that we should distinguish between local microclimates (i.e., air temperature measured in microhabitats) and fine-grained microclimates (i.e., the temperature of surfaces of the various elements composing the microhabitat). The use of one or the other of these two 'metrics' mostly depends on the body size of the focal organism and therefore on the spatial scale at which one should look at the biophysical processes.

Air temperature for weather records is typically measured at a standard height of 1.5m above ground, in open areas. *Local* microclimates often are characterized by measuring air temperature in various microhabitats and by comparing to the standard

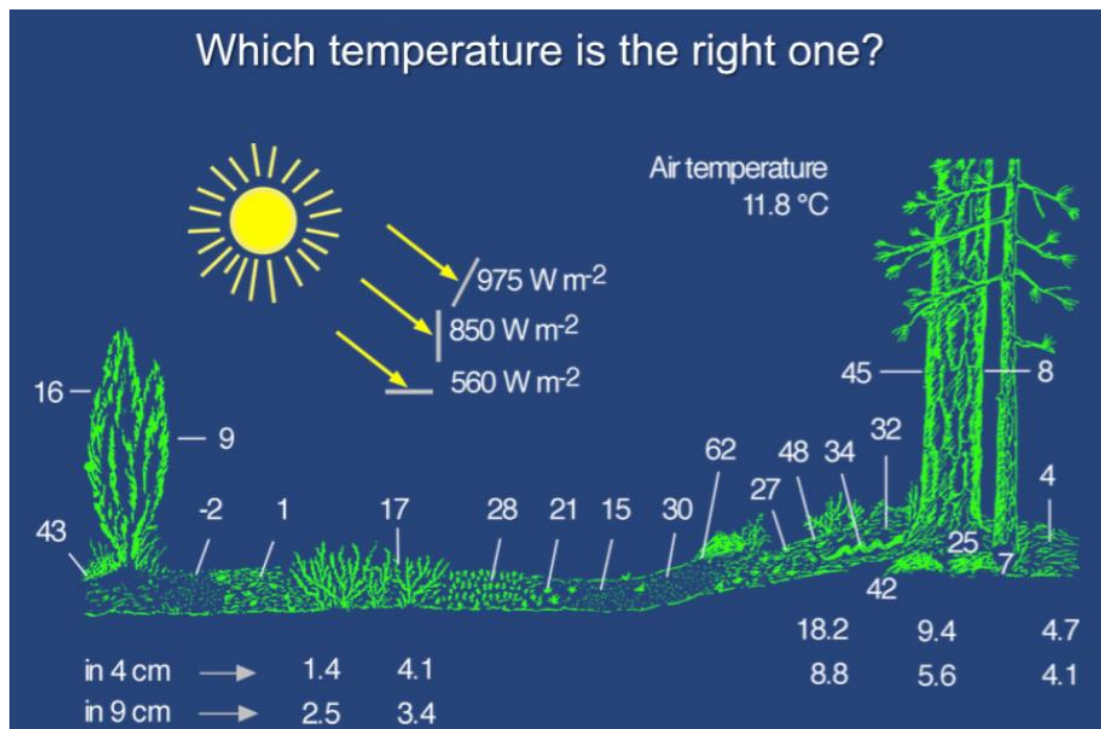


air temperature. In general, botanists make these measurements by comparing air temperature 1.5m above ground and close to the soil, as well as within the first layers of soil where plants develop their roots. For example, shading by the woodland leaf canopy reduced maximum temperatures in the understory by 5°C in September, compared to other habitat types such as grassland in the UK (Suggitt et al. 2011). In this study, the absolute maximum temperature recorded in woodland in September did not exceed 25°C, whereas temperatures in excess of 35°C were recorded in grassland. In another study, in the middle of a sunny day in summer in UK, wood-land air temperatures were lower than grassland and decreased from the canopy-top to the understory (Morecroft et al. 1998). The maximum difference between wood-land and grassland air temperature was about 3°C. In addition, several studies focused on topoclimates which are meteorological air temperatures distributed across the landscape depending on slope and aspect of the terrain, again revealing temperature deviations of 5-10°C among different areas a complex landscape (Holden et al. 2011; Sears et al. 2011). In these and other similar studies, authors highlighted the significance of the amplitude of temperature differences among habitats which often surpassed the amplitude of climate warming predicted for 2100.

Nevertheless, these temperature deviations reported at local scale may even be well below what happens at very fine scale which matters for tiny ectotherms such as most arthropods. The old literature (60s to 80s) is relatively rich in examples indicating the extent to which the temperature in fine scale microclimates can deviate sometimes strongly from ambient air temperature (Figure II.6). Stoutjesdijk (1977) reported a 'snapshot' of surface temperatures measured at the end of winter in Holland. While (meteorological) air temperature was about 12°C, some surfaces reached ~60°C, e.g. decaying grass tussocks, and other were freezing, e.g. humid litter in the shade (Figure II.6) (see also Stoutjesdijk & Barkman 2014). These thermal differences are linked to simple physical processes including the cosine law of illumination which provides the incident radiation level at a given surface from its slope and the direct beam of (solar) radiation (Oke 1987), evapotranspiration from the surface such as vegetation (Jarvis 1976), and boundary layer effects that provide limited homeothermy to some structures like forest understory (Finnigan 2000). The bark surface of trees when exposed to full sun can reach extreme temperatures near 50°C for oak bark when air temperature is near 15°C (Nicolai 1986). Making the



analogy with the comparison of local scale temperature variations and the predicted amplitude of regional warming (previous paragraph), I am unsure that an amplitude of warming of 30-40°C can be compared to anything, except geothermal ponds (Dunckel et al. 2009) or hydrothermal vents (Kashefi & Lovley 2003)!



**Figure II.6.** Illustration of the surface temperature deviations across a microhabitat (elements are not to scale). Originally (Stoutjesdijk 1977), this figure reported a transect across the south-facing edge of a pinewood and adjacent heathland with Juniper shrub (measurements made on 3 March 1976, 12.00-12.00 h with an easterly wind of 5 m/s at 10 m height). Soil temperature was measured at 4 cm and 9 cm. Bare sand: stippling, litter: hatched. Adapted from Stoutjesdijk 1977 by Körner 2013.

In addition to the amplitude of the thermal deviation, fine-scale microclimates are also characterized by a potentially large spatial heterogeneity at small scale. In the example of tree trunk bark temperature above, Nicolai (1986) also reported large temperature differences within the surface of rugose trunks, between the 'valley' (depression of the bark surface) and the 'hill' (bumps), with differences of ~10°C over few centimeters. These microclimatic patterns at the bark surface determine the frequency and abundance of oribatid mites (Nicolais 1986). A similar temperature range (~10°C) is observed over few cm between underneath rocks exposed to the sun

and the soil substrate in Australia, where the flat-rock spider female finds optimal warm conditions for hunting while the eggs benefit from the cooler environment offered by the substrate (Pike et al. 2012). Again, a roughly similar amplitude was observed ( $\sim 10\text{-}15^\circ\text{C}$ ) in the maximal body temperature of mussels in the rocky intertidal at low tide across a single mussel bed of less than 1m (Denny et al. 2011; Dowd et al. 2015). Indeed, this body temperature range at fine scale rivaled and sometimes greatly exceeded the expected difference in body temperatures along  $\sim 1600$  km of the western coastline of North America (Denny et al. 2011 versus Helmuth et al. 2006). Finally, in plant crops, a vegetation surface temperature range of almost  $20^\circ\text{C}$  was observed within the first meter, implying that insect pests can encounter quite various thermal conditions within such a small scale, although no clear relationship emerged between fine scale thermal variation and the abundance of pests (Faye et al. 2017). To conclude, the variety of thermal conditions across fine scales can be high in various ecosystems. This variability can potentially select or generate as much variability in thermal limits or other thermal biology traits among individuals at such fine scales in ectotherms. Yet, few studies quantified the inter-individual variation in thermal traits in field populations at such a fine scale. For example, Franken et al. (2018) report variations of  $\sim 10^\circ\text{C}$  in the CTmax of springtails and spiders in sand dunes. Unfortunately, these authors did not measure fine scale variations in sand surface temperature.

### *c) Modeling microclimates*

Developing microclimate models generates predictive tools especially in the context of quantifying the impact of climate change on the conditions experienced by species in their microhabitat. Again, biophysical principles can be applied to compute the energy and mass exchange between the atmosphere and the different elements of the environment that generate the microclimate of species (Kearney & Porter 2009). This past decade has seen the emergence of several microclimate models. Certainly, the most famous microclimate toolbox is the microclimate model integrated into the *NicheMapR*, a suite of programs for mechanistic modelling of heat and mass exchange between organisms and their environments (Kearney et al. 2013, 2014; Kearney & Porter 2016). This microclimate biophysical model is designed to predict hourly above- and below-ground conditions from meteorological, terrain, vegetation and soil data (Kearney & Porter 2016). The model also includes routines

for computing solar radiation, including effects of shading, slope, aspect and horizon angles (hillshade), and can include variable substrate properties with depth. *Microclima* is another biophysical model available to obtain provide hourly estimates of near-ground air temperature at variable resolutions (e.g., as low as 1 m<sup>2</sup>) to work at both micro and meso-scales (Maclean et al. 2019). The *microclima* package (in R) is flexible and efficient and provides an accurate method of modelling fine-scale variation in temperature. This model was used to reveal spatial variations in warming caused primarily by a decrease in daytime cloud cover with a resulting increase in received solar radiation, and secondarily by a decrease in the strength of winds, which has amplified the effects on temperature of solar radiation (Maclean et al. 2017). Other models are available but at lower temporal/spatial resolution and/or they are based on statistical approaches that make them less powerful than biophysical models (e.g., Gunton et al. 2015; Levy et al. 2016). In general, all these models open new avenues for microclimate-based macrophysiology (Duffy et al. 2015). To date, however, no model has been developed to accurately capture the microclimate heterogeneity such as the ones I detail above at very fine scale. In other words, we are still missing the implementation of microclimate modeling to most of the biodiversity which lies at small body size (the peak of biodiversity has a body size of 3-10mm in length with theoretically has much species below than above this range; May 1988).

*d) The impact of climate change on microclimates*

The next challenge for ecologists (in collaboration with climatologists) is to predict the amplitude of micro-climate change for the future. This prediction is important to further produce accurate simulations of the impacts of climate change on future species distributions, population trends and extinctions. This is clearly a crucial component for conservation biology in a changing climate (Shi et al. 2016). The microclimate models developed so far (see previous section above) were used to predict the dynamics of microclimate temperature and its biological consequence for relatively large ectotherms (e.g., Kearney et al. 2018) and/or at a theoretical spatial scale that is difficult to connect with the fine scale microclimates observed in the natural habitat (e.g., Sunday et al. 2014). The only study I am aware of that *directly* and *biophysically* quantified how much of atmospheric warming is transferred into fine scale microclimate comes from the community of intertidal ecologists more than

10 years ago (Gilman et al. 2006). In this study, a biophysical model of body temperature of Californian mussels was used to show that a simulated 1°C increase in air or water temperature increased the maximum monthly average of daily body temperature maxima by 0.07–0.92°C, depending on various parameters including the geographic location and the vertical position in the rocky intertidal. Based on climate change scenarios for 2100, Gilman et al. (2006) calculated increases in monthly average maximum body temperature of 0.97–4.12°C, again depending on geographic and rocky intertidal locations — warming amplitude values that do not match exactly the atmospheric warming amplitude. Therefore, the geographic variation in body temperature sensitivity (more a mosaic than a South-North linear gradient) can modulate species' experiences of climate change and must be considered when predicting the biological consequences of climate change.

Most studies dealing with the impact of climate change on microclimates provide *indirect* evidence, therefore with less precise quantification compared to the study of Gilman et al. (2006). Nevertheless, these studies provide solid inference that most microclimates will help ectotherms to buffer at least a significant part of the amplitude of global warming. For example, the forest understory is well recognized to buffer atmospheric thermal variations. Quite interestingly, several studies indirectly inferred this buffering ability by analyzing the thermal preferences of plants that prosper on the forest floor across Europe (De Frenne et al. 2013; Lenoir et al. 2013). The maximal temperature within forest covers can be ~5°C cooler than adjacent open areas but this buffering ability depends greatly on the local hydrology and the water balance of trees (Davis et al. 2019). Similar buffering effect was found in plant community changes in grasslands on North-facing slopes in complex terrain where the amplitude of historical warming was lower (Maclean et al. 2015). More generally, a systematic analysis of forest versus open area air temperatures showed that forests function as a thermal insulator, cooling the understory when ambient air temperatures are hot and warming the understory when they are cold (De Frenne et al. 2019). This implied also that the latitudinal gradient of forest-floor temperatures is less steep than the latitudinal gradient in macroclimate temperature (De Frenne et al. 2019). A similar global approach focusing on local microhabitats (soil, logs, epiphytes and tree holes) across the vertical gradient of tropical forests showed that microhabitats buffered temperature by ~4°C and reduced maximum temperatures by

about the same amplitude (Scheffers et al. 2014a,b). Buffering was most pronounced in tropical lowlands where temperatures were most variable (Scheffers et al. 2014a).

These studies focused on the buffering ability of microclimates, but curiously no example is provided in the literature about a microclimate that could magnify the amplitude of climate warming. *Magnifiers* may be widespread in the natural environment, including flowers that warm above ambient air when receiving solar radiation (Dyer et al. 2006) or flowers that produce heat (Seymour et al. 2003), enclosed structures such as galls and leaf mines (Layne 1993), and the pitcher of some carnivorous plants (Kingsolver 1979). In addition, several studies called for the inclusion of 'fine scale' weather and climatic data into species distribution models (Filz et al. 2013; Lembrechts et al. 2019) or vulnerability assessments (Storlie et al. 2014) to account for the buffering ability of some microhabitats. But again, most of the biodiversity is living at a much finer scale. There is evidence that even within these buffering microhabitats (grasslands, forests), finer scale patches show great thermal heterogeneity including plant surfaces that are sometimes warmer than ambient air temperature (Leuzinger & Körner 2007; Scherrer & Körner 2010).

*e) The leaf microclimate*

Collectively, leaves are among the most important microhabitats in the biosphere. Leaves are, foremost, plant organs for gas exchange and energy capture. The leaf system is probably the most important biological unit linking the global climate (e.g. evapotranspiration, carbon dioxide assimilation) and the functioning of ecosystems (e.g. recycling of nutrients). Leaves are also home to an enormous diversity of other organisms, from bacteria to arthropods, spanning several functional groups and trophic levels – symbionts, parasites, herbivores, predators, parasitoids etc. (Preece & Dickinson 1971; Strong et al. 1984; Juniper & Southwood 1986; Meyer & Leveau 2012). This relationship between the host plant leaf and associated organisms has been extensively studied from evolutionary (e.g. phylogenetic associations between herbivores and host plants) and ecological perspectives (e.g. the nutritional ecology of herbivore insects and plant defenses) (Labandeira et al. 1994; Lewinsohn et al. 2005; van Loon et al. 2005; Wilf et al. 2006). Fewer researchers have attempted to describe and explain how organisms interact with their host plant leaves from the perspective of environmental biophysics. From a purely physical point of view, the leaf surface is a highly characteristic microhabitat, as the abiotic

conditions within the leaf boundary layer can differ markedly from those in ambient air (Willmer 1986; Boulard et al. 2002). For these reasons, the leaf microclimate is my biological model of predilection. **In this dissertation (see *Part III: My scientific production*), I point out the crucial role of leaf microclimates in the fate of leaf-dwelling organisms in a changing climate.**

Significant deviations between macro- and micro-climates at the surface of vegetation are quite common (Gates 1968; Helliker & Richter 2008; Porter et al. 2009; Scherrer & Körner 2010). In particular, the temperature at the leaf surface and in surrounding air can differ markedly (Linacre 1964, 1967; Chelle 2005). The influence of leaf microclimates on organisms depends on organismal body size. Large organisms such as last-instar sphingid caterpillars (Lepidoptera) are more influenced by ambient conditions than leaf microclimatic conditions (Casey 1976; Woods 2013). By contrast, small arthropods at the leaf surface are more likely to be completely embedded within the leaf boundary layer (Woods 2010), although this interaction was never fully investigated. These tiny organisms should experience leaf temperature surface variations rather than ambient air directly. Also, water vapor pressure is higher within the leaf boundary layer compared to ambient (Willmer 1986). Organisms at the leaf surface experience these abiotic conditions within the leaf envelope, but this is only rarely considered in studies looking at the effects of climate variations on leaf-dwelling organisms, with a few notable exceptions. North American pitcher plant mosquitoes are adapted to variations in their pitcher leaf microclimate, which magnify the daily air temperature increase (Kingsolver 1979), rather than to ambient summer or winter weather conditions (Bradshaw et al. 2000). Moth eggs in an Arizona desert avoid lethally high temperatures by developing on host leaves that transpire away significant heat (Potter et al. 2009). Such links between an organism's thermal requirements and how it uses or manipulates leaf filters probably are widespread.

Adding the leaf microclimate as a factor when studying the response of organisms to climate change cannot be done without adding complexity. Leaf microclimates, which include temperature and humidity at the leaf surface, result from the biophysical filtering of local macroclimates by the plants themselves through complex, nonlinear processes (Campbell & Norman 1998; Nobel 1999). These processes can be integrated into the heat budget of a leaf, which computes leaf temperature from the characteristics of its physical environment (Gates 1980; Jones

1999; Nobel 1999). Briefly, the balance between radiative energy absorption and heat losses during convection and evapotranspiration drives the leaf-to-air temperature deviation at short time scales (Schuepp 1993). Most of the knowledge on leaf heat budget balance model was acquired decades ago by micrometeorologists and plant ecophysiologicalists but has not yet played a central role in studies by ecologists working on climate change (Woodward et al. 1995; Hanson et al. 2005; Michaletz et al. 2015, 2016). More work on the potential effects of climate change on the leaf energy budget has been done by agroecologists (Challinor et al. 2009). Nevertheless, a mechanistic approach provides a strong background for placing the abiotic environment actually experienced by leaf-dwelling organisms into models of the ecological effects of climate change.



## *Part III.*

### Synthesis of my scientific production

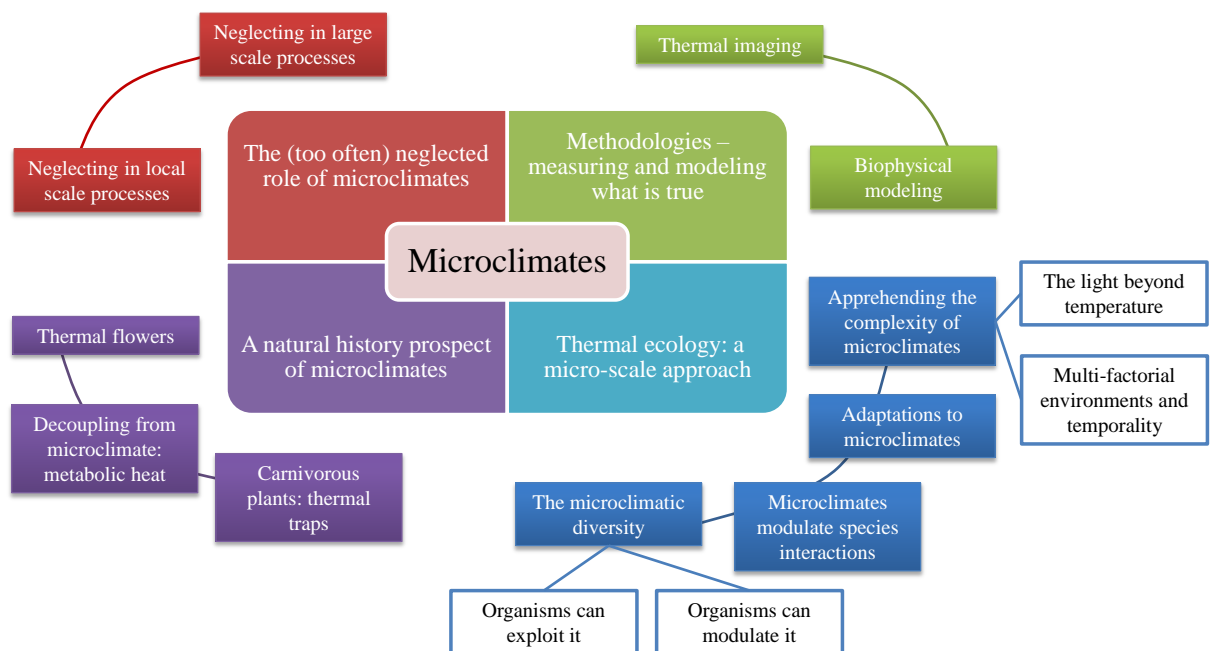
*This section gives a synthetic view of my research that was published in scientific journals. This synthesis is topic-oriented rather chronologically framed. My aim is to integrate all my studies in a coherent fashion, to reveal a structure that may not be obvious otherwise.*



A weevil watching an UFO (Unidentified *Fotographing* Organism, i.e., me) from the leaf surface in the tropical forest of Ecuador. © Sylvain Pincebourde.

## 1. A general view of my research: jigsaw falling into place

Fundamentally, I am an ecologist attempting to understand the relationships between organisms and their environment (both biotic and abiotic). The specificity of my research lies in the scale at which I work to depict the mechanisms that underpin these relationships. Most ectotherms are small enough to live under physical environments that differ fairly from what humans experience in terms of, for example, viscosity (Reynolds number), boundary layers and temperature. Therefore, the pertinent scale at which one can hope to comprehend the mechanisms of arthropod life is the micro-scale which I define here as the length-scale corresponding roughly to body size (see *Part II: overview of the field*). The term *microclimate* is appropriate here to characterize the environmental conditions that impose constraints on ectotherm and drive their ecophysiology. Ultimately, the pertinent variable is the body temperature of the ectotherm which I include in the term microclimate. I deal with the role of microclimates in ectotherms' life with an integrative approach—well, the approach of an ecologist. My pathway may appear relatively eclectic at first. All my work, however, falls into four main themes that are centered on the key topic of the role of microclimates in ectotherms' life (Figure III.1).



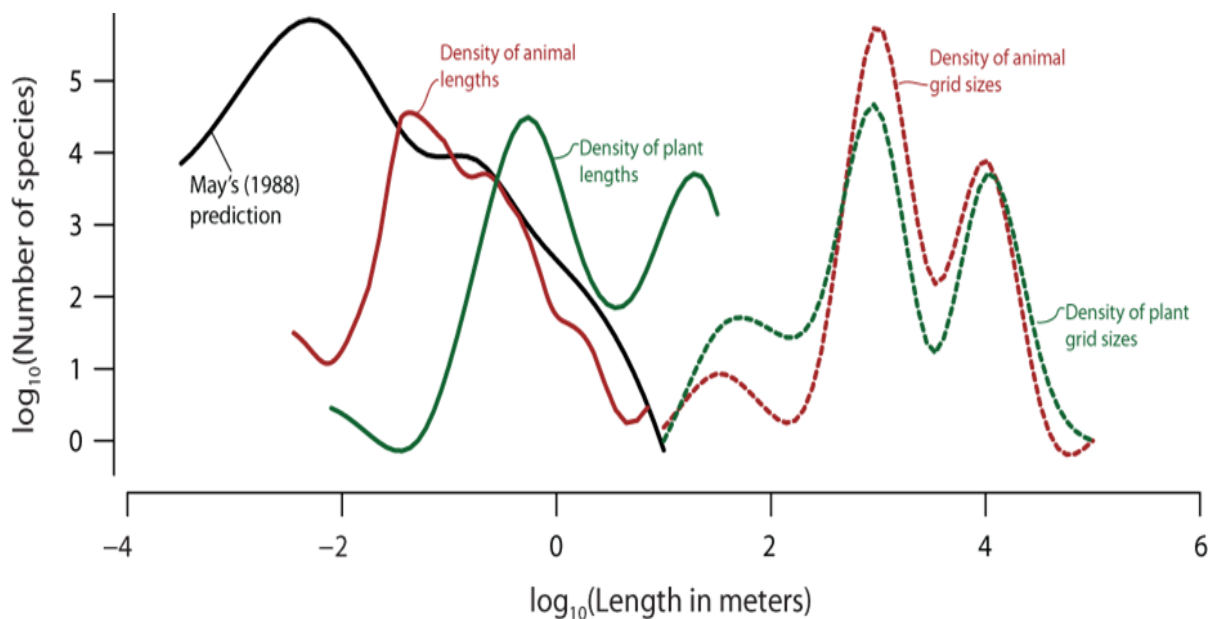
**Figure III.1.** The different facets of my research topics around the theme of microclimates.

The fundamental research on thermal ecology is partitioned into several sections (Figure III.1), from a descriptive approach of the microclimatic diversity to the role of microclimates in modulating species interactions and driving thermal adaptations, and to the hot question of how we can integrate the complexity of microclimates into a single framework. This research inevitably involves specific methodologies including thermal imaging and biophysical modeling to which I contribute to develop further. In addition, I frequently have a critical look over studies that investigate ecological processes at various scales by neglecting microclimates: what are the consequences potentially of ignoring microclimatic conditions of ectotherms? Finally, as an ecologist in love of Nature, I initiated what I call a natural history prospect of microclimates: the way particular natural histories generate specific microclimates such as thermogenic flowers and the pitcher of some carnivorous plants. At first, this last section may look as an unstructured list of random items, but these aspects (will) also link thermal adaptations and microclimates (see *Part IV: Research perspectives*). The work I detail below refers to most of my publications that appear in blue in the reference list (see *References*).

## 2. The (too often) neglected role of microclimates

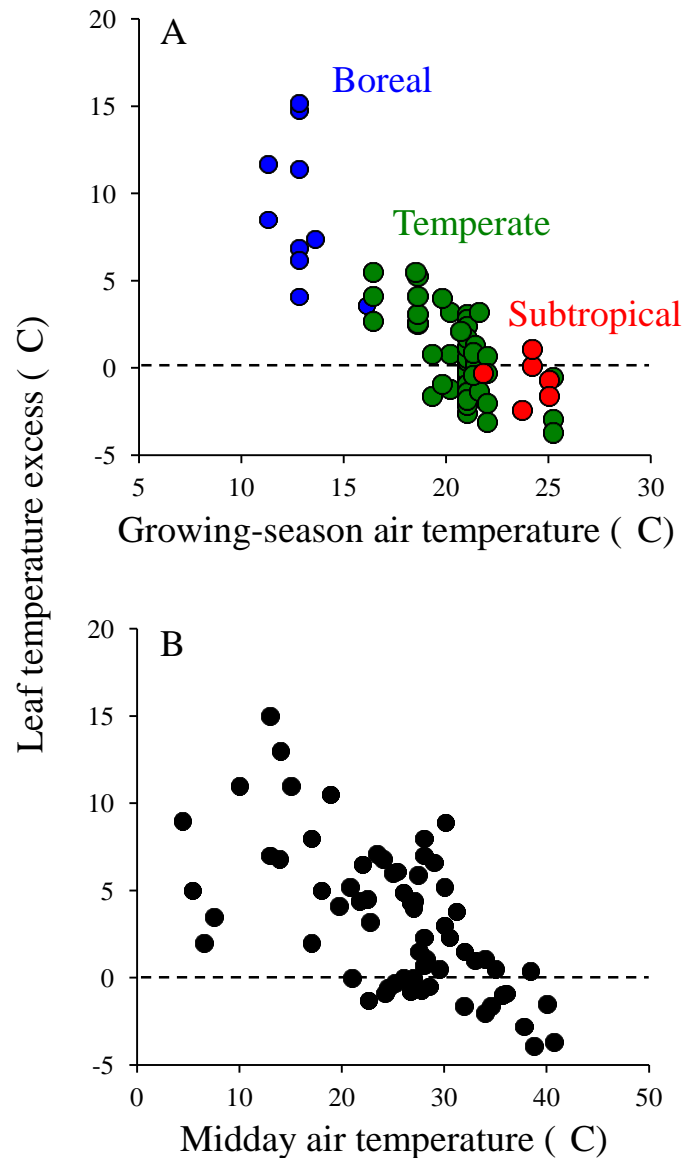
While the importance of microclimatic issues has been acknowledged and demonstrated by a subset of ecologists since almost a century, most macro-ecological studies do not include microclimates when looking at large scale processes. A striking example is the use of species distribution models, which basically use climatic data taken at broad spatial scale to determine the distribution of the climatic niche of species. Exceptions exist, however (Kearney & Porter 2009). Although this problem was recognized by a significant portion of ecologists, it was never clearly demonstrated and quantified before. I collaborated with Prof. Arthur Woods and his postdoc Kirsten Porter to analyze a set of published studies that used species distribution models on various types of organisms (**Potter, Woods & Pincebourde 2013**). For each study, we extracted the spatial scale at which the climatic data were taken as well as the body size of the studied organism(s). Not surprisingly, researchers mainly use climatic variables measured or predicted at large scale,

typically corresponding to the resolution of the main climatic databases (grid cells of 1 km and 10 km; e.g., WorldClim). The deviation from the scale of body size is therefore extreme on average, ca. 10,000-fold larger than the animals they study, and ca. 1,000-fold larger than the plants they study (Figure III.2). These macro-ecological procedures totally erase the spatial heterogeneity of microclimates that exists at all scales between body size and the coarse resolution of climatic data providers. The problem is even more perfidious as it is not clear if coarse scale climatic data represent a spatial/temporal average over the grid cell or a median of the distribution or something else (Faye et al. 2014). This study published in *Global Change Biology* attracted a lot of attentions and citations, showing that ecologists are more and more aware of this problem.



**Figure III.2.** Lengths of grid cells from published species distribution models (SDMs) compared to the lengths of the animals and plants they studied. The black density plot is a spline fitted to data from May's 1988 study (May 1988), which represents his estimate of the body size distribution of all terrestrial animals. Density plots of the rest of the terrestrial data are shown for animals and plants separately. The two peaks in the grid-size density plots correspond to the commonly used grid scales of 1 and 10 km (e.g., these were the most common resolutions exported from the WorldClim database few years ago). The distribution of terrestrial animal sizes was significantly shifted toward large body sizes compared to May's predicted distribution. The distributions of animal and plant grid sizes were not statistically distinguishable.

Although the spatial scale mismatch illustrated above is intuitively comprehensive, a similar questioning gives surprises when applied to more local scales. To what extent is our knowledge on the mechanisms operating at local/small scale sufficient to predict with confidence the impacts of climate change? With Prof. Arthur Woods, we applied this question to a system we know well: the leaf microclimate (**Pincebourde & Woods 2012**). The drivers of leaf temperature, both environmental and ecophysiological, are all relatively well described (see *Part II: overview of the field*). But the more we learn on the functioning of the processes that regulate leaf temperature, the more it brings uncertainty on the impact of future climate change on leaf temperature patterns. In particular, the stomatal behavior is at the interface of numerous responses: they respond to environmental factors, biochemistry of the leaf, water status, leaf age, activity of herbivores etc. It is however urgent to better comprehend how stomata respond to environmental fluctuations as well as to the damages caused by phytophagous arthropods and pathogens to leaf tissues. Then, a macroecological pattern of tree leaf temperature was identified (Helliker & Richter 2008): despite an increase in atmospheric temperature from boreal to sub-tropical latitudes, the mean leaf temperature of trees remains remarkably constant globally (around 23°C). This implies that the leaf temperature excess is important at high latitudes (i.e., the leaf is warmer than ambient air) and close to zero or even negative at low latitudes (i.e., the leaf is at the same temperature than ambient air or even cooler) (Figure III.3). This study (Helliker & Richter 2008), however, remains a bit controversial because empirical measurements do not really support these quantitative predictions (Figure III.3). Indeed, Helliker & Richter inferred this latitudinal gradient of tree leaf temperature by measuring an oxygen isotopic composition in wood tissues. Their metric corresponds to the temperature of leaves when they were photosynthesizing in the sun during the day, as averaged over the tree canopy (but mostly leaves exposed to the sun) and over the tree lifetime (i.e., >30 years). Their conclusion is therefore difficult to integrate and compare to actual measurements of tree leaf temperatures.



**Figure III.3.** Global trends in leaf temperature excess via two distinct approaches. (A) Leaf temperature minus ambient growing-season temperature is shown as a function of ambient growing-season temperature for different latitudes (boreal, temperate and subtropical regions) and for 39 tree species. Leaf temperatures correspond to averages over growing season. They were resolved by analysis of the oxygen isotopic ration in the cellulose. Redrawn from data provided in the supplementary materials by Helliker & Richter (2008). (B) Midday leaf temperature minus midday ambient air temperature is shown as a function of the midday ambient air temperature in 70 plant species from different localities and including greenhouses. Data points are instantaneous temperature measurements. Redrawn from data provided by Linacre (1967).

Given this lack of certainty on the potential impact of climate change on the latitudinal gradient of leaf temperatures, we developed two conceptual hypotheses in

2012 (**Pincebourde & Woods 2012**). The ‘*differential-buffering-ability hypothesis*’ states that the amplitude of temperature change at the leaf surface will be negligible in the tropics compared to higher latitudes. Leaves at low latitudes are already adapted to dampen the effects of elevated air temperature. These leaves can therefore buffer future warming, as long as the amplitude of the warming does not exceed their buffering abilities. By contrast, leaves in temperate and boreal areas are more adapted to *magnify* environmental fluctuations. The surface temperatures of high-latitude leaves will therefore increase about as much as does the ambient air. Leaf-associated organisms will therefore experience warming at the leaf surface mostly at high latitudes, leading subsequently to accelerated development of insects at first, and further to mortality events once leaf surface temperature reach the thermal limits of insects. In general, according to this differential-buffering-ability hypothesis, global change is likely to cause important ecological effects at high latitudes, where the leaf microclimate will change the most, whereas the direct effects could be negligible in tropical regions.

By contrast, the ‘*fluctuation-adapted hypothesis*’ proposes that climate-driven ecological shifts will be more important at low rather than at high latitudes. Leaves in boreal and temperate latitudes are already adapted to highly fluctuating environments, whereas leaves in the tropics are not. Compared to (sub)tropical leaves, therefore, temperate leaves should be preadapted to cope with even larger temporal fluctuations (note that several years after this publication, I realize that this matches the climate variability hypothesis; Vasseur et al. 2014). Even if the amplitude of the temperature change is more pronounced at high latitudes, plants and leaf-dwelling organisms are already adapted to such levels of thermal variance. By contrast, increasing the temperature variance at low latitude, where organisms live in general near their temperature tolerance threshold (Dillon et al. 2010), would cause chronic thermal stress and temperature-induced mortality events. This hypothesis implies that slower warming in the tropics would have higher ecological consequences than at temperate latitudes.

The outcome of these two hypotheses largely depends on the thermal limits of ectotherms along the latitudinal gradient. We start to realize that the variability in thermal limits is larger at local scale than globally (**Pincebourde & Casas 2019**; see below), which helps reducing the uncertainty by redirecting our analyses to the local scale rather than macroecological scale (Sunday et al. 2011). Also, recent advances



in plant ecophysiology further reduce this uncertainty in climatic conditions at the surface of leaves. A general pattern of acclimation and adaptation of the stomatal system might emerge. Plant species have reduced their maximal level of stomatal conductance in response to increase atmospheric CO<sub>2</sub> over past decades, owing to a reduction in the size and number of stomata (Lammertsma et al. 2011). A modelling approach also showed that this reduction in maximal stomatal conductance would continue as atmospheric CO<sub>2</sub> keeps increasing, until the plants reach the limits of their plasticity (DeBoer et al. 2011). Reduced maximal stomatal conductance not only leads to lower transpiration rates and warmer leaf surfaces in general but also diminishes the relative importance of short-term stomatal responses to environmental fluctuations.

*Conclusion* - Most ecologists are aware that the microclimatic conditions matter much for ecophysiological mechanisms in ectotherms. Yet, the field of macroecology only rarely integrates the environmental conditions taken at fine-scale. Very recent progress was made however including modeling frameworks and empirical datasets that are made available for ecologists. Nevertheless, these tools remain positioned at a relatively coarse spatial scale compared to the microscale processes I am studying and that are reported below. Macroecology should meet micro-scale processes to develop a form of 'total ecology', which is necessary now to respond to the grand environmental challenge that our society is now facing.

### **3. Thermal ecology: a micro-scale approach**

The field of thermal ecology is emerging in the context of global change biology as it brings powerful concepts and tools (thermal biology) to predict ectotherms' responses (See *Part II: Overview of the field*). During my research, I contributed to the development of this field by investigating the micro-scale processes of interaction between ectotherms and their environment. This research articulates the following questions:

- What is the diversity of microclimates available for ectotherms?
- How ectotherms can modulate their microclimates?

- Can organisms exploit this diversity to behaviorally thermoregulate?
- How available microclimates modulate species interactions?
- To what extent are organisms adapted specifically to their microclimate?
- How can we apprehend the full complexity of microclimates in space/ time?

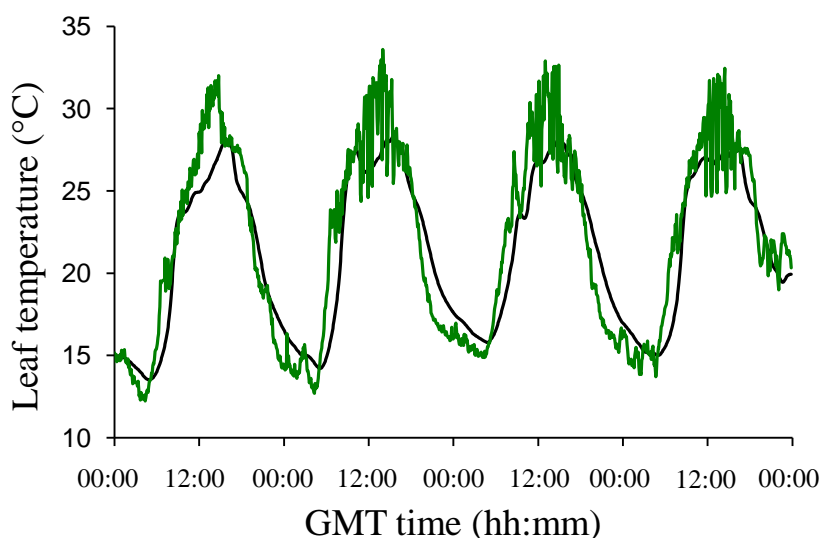
Below, I explain what my research provides to these specific questions.

*a) The microclimatic diversity in space and time*

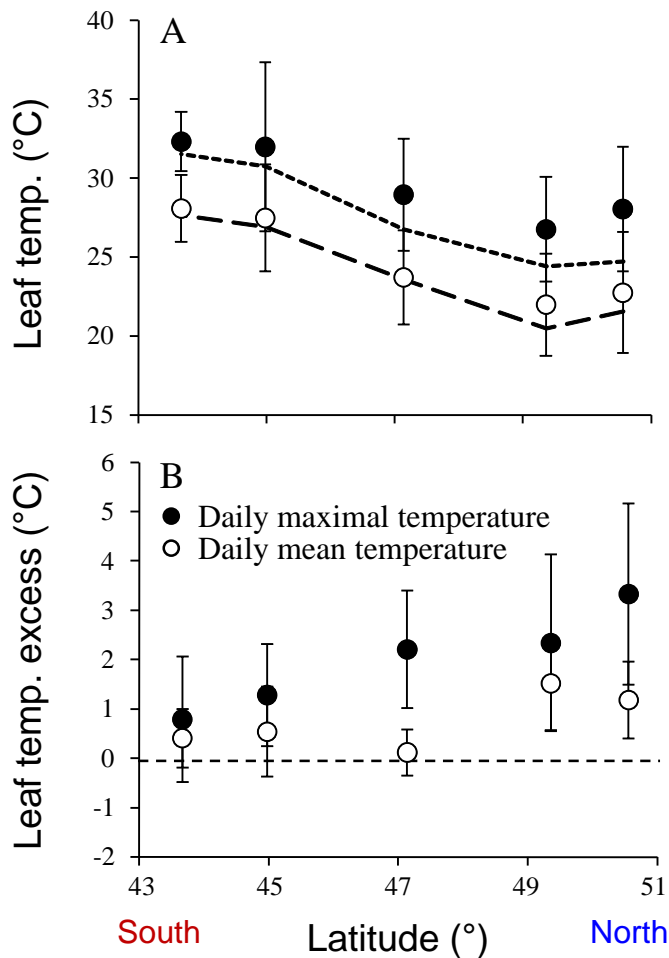
Forecasting the impacts of future climate change on organisms requires that we understand more generally how microhabitats filter environmental fluctuations and whether the heterogeneity at small scales will be sufficient to allow organism to find and exploit favorable conditions (Kearney et al. 2009; Hannah et al. 2014; Sunday et al. 2014). Macroclimates interact with living and non-living objects in the environment to produce a complex mosaic of thermal microclimates. Although the generation of such mosaics is conceptually straightforward (e.g. the distribution of surface temperatures across space and the changes over time), there still exists no general framework for predicting spatial and temporal patterns of microclimatic variation. In collaboration with Prof. Arthur Woods (Univ. Montana) and Prof. Michael Dillon (Univ. Wyoming), we developed a simple way of dealing with these microclimatic mosaics by analyzing them along three axes (**Woods, Dillon & Pincebourde 2015**): (i) the nature of the object producing the microclimate (abiotic versus biotic), (ii) how the microhabitat translates atmospheric variations (magnify versus buffer), and (iii) the spatial scales over which microclimatic conditions vary (long versus short). These three axes define the complexity, heterogeneity and uncertainty of microclimates in a changing world.

The microclimate at the leaf surface is an excellent example of a biotic object producing a particular thermal environment at its surface. Various parameters of the leaf are influencing the temperature of its surface including shape, size, optical properties, inclination angles, and stomatal behavior (see *Part II: Overview of the field*). Across the years, I have measured the surface temperature of apple leaves under various conditions and for different purposes (**Pincebourde et al. 2007**; **Caillon, Suppo, Casas, Woods & Pincebourde 2014**; **Pincebourde et al. 2017**). The most striking feature of apple leaves at temperate latitude (near Tours) is that leaf temperature at midday is higher than ambient air by several degrees when in full sun, while it is slightly lower than ambient air during the night (Figure III.4).

Therefore, the leaf microclimate magnifies both warmest and the coldest air temperatures, thereby increasing the thermal variance compared to the atmosphere. The thermal variance for leaves in the shade remains of course close to that of ambient air because solar radiation is the driver of the leaf temperature excess relative to ambient air. Then, we wanted to quantify this magnifying effect across a latitudinal gradient. According to the hypotheses developed above (from Helliker & Richter 2008), we expected apple leaves at low latitude (towards equator) to deviate from air temperature much less than leaves upper North. This test was part of the PhD of Robin Caillon that I co-supervised (at 90%) with Prof. Christelle Suppo (10%). We quantified the latitudinal gradient of leaf temperature patterns by measuring apple tree leaf temperatures at a high temporal resolution at five sites along a latitudinal gradient of ~750km during two growing seasons ([Caillon & Pincebourde in prep](#)). A clear latitudinal gradient of leaf temperatures was evidenced, and it differed from the air temperature gradient, in particular when analyzing the daily maximum temperature (Figure III.5). The ability of leaves to buffer part of the air temperature change along latitude varied between months and also between different exposures within the tree canopies. Therefore, there is no single latitudinal gradient for leaf temperature. Instead, the level of exposure to solar radiation and its intensity both set different latitudinal gradients for leaves in the sun and leaves in the shade.



**Figure III.4.** Illustration of a temporal series of leaf temperature (green line) during four consecutive days. The black line shows the air temperature trace. Leaf temperature was measured on apple using a thermocouple. Leaf temperature peaks are caused by variations in solar radiation level.



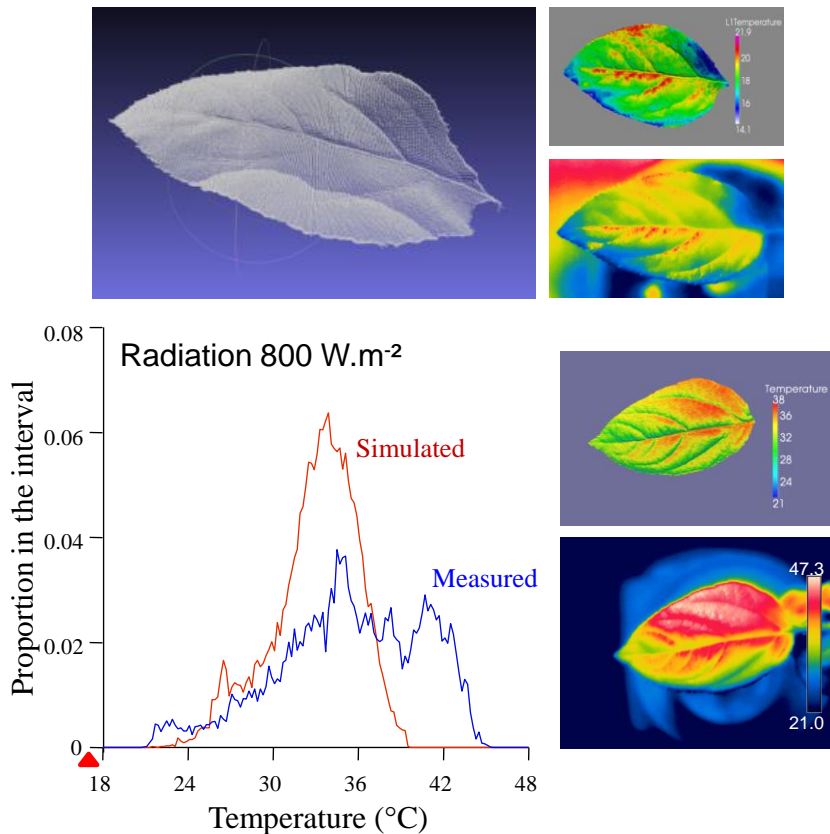
**Figure III.5.** The latitudinal gradient of apple leaf temperature for the month of July. (A) The mean daily leaf temperature (white circles) and the daily maximum of leaf temperature (black circles) are shown for each month. The mean daily air temperature and the mean daily maximum air temperature are represented by dashed and dotted lines, respectively. (B) The leaf temperature excess (leaf temperature minus air temperature) is shown as both mean daily excess (white circles) and mean daily maximum excess (black circles).

A plethora of parameters has to be known to run the heat budget model of a plant organ. We attempted to rank these parameters according to their relative weight on leaf surface temperature distributions at the tree canopy scale and at the forest stand canopy scale (Woods, Saudreau & Pincebourde 2018). We used again the biophysical model of apple leaf temperature, and we played with it asking to what extent one can predict leaf temperature distributions at the whole tree canopy. We also investigated the extent to which the sampling of temperature distribution at the surface (2D) of forest canopies alone (i.e., like remote sensing would do) can be used to infer the entire leaf temperature distribution of 3D canopies. A Morris sensitivity

analysis was used to explore our large parameters space. In our case, we used 13 parameters and variables with four levels each, or  $4^{13} = 67,108,864$  unique combinations of values. Exploring the total factorial space is effectively impossible. The Morris approach cuts down on total coverage by taking a kind of random but well-distributed walk through the 13-dimensional hypercube of parameter values. We explored only 5,600 unique parameter combinations—which is  $<0.01\%$  of the total number—but were still able to identify the relative influence of individual parameters on simulation outcomes. Our study reported that overall, not surprisingly, climatic factors have the greatest effects on leaf temperature distributions. However, we found that structural parameters (e.g., leaf area density and general shape of the crown) have a greater influence than physiological parameters (e.g., stomatal conductance and stomatal responses to environmental parameters) that tend to receive the most empirical attention. Moreover, our theoretical approach showed that remote sensing (i.e., measurements of leaf temperature distribution at the top of the canopy) is adequate to estimate overall 3D forest canopy distributions of leaf temperature within reasonably large parameter ranges and at the scale of our study (the subunit of the model was voxels of 20cm).

These studies above considered the mean leaf surface temperature. Nevertheless, the surface temperature of a single leaf can be spatially heterogeneous (Leigh et al. 2017). The mechanisms generating the within-leaf thermal heterogeneity were not clear before our study. The wind-edge effect (the leaf is cooled at the edge attacked by the wind vector) was thought to be the main driving force (Roth-Nebelsick 2001). However, slight changes in leaf angle relative to the position of the sun are sufficient to cause large surface temperature shifts in general (Oke 1987). Therefore, we hypothesized that the leaf microtopography plays a role in temperature variations across a single leaf surface. We tested this hypothesis by developing a biophysical model of heat transfers across the leaf and with ambient air based on the distribution of leaf angles across its surface (Saudreau, Ezanic, Adam, Caillon, Walser & Pincebourde 2017). The microtopography of a set of apple leaves was scanned with a high spatial resolution to feed the mechanistic model. Then, the model outputs (i.e., thermal map of single leaf surfaces) were compared with thermal images of single leaves taken under various climatic conditions in the lab (Figure III.6). We revealed that the heterogeneity of surface temperature within single leaves can be up to  $20^{\circ}\text{C}$  under extreme but realistic circumstances (low wind

speed, high radiation load, although with moderate air temperature and relative humidity). More generally, we report leaf surface temperature ranges of 10-15°C under typical conditions both with the model and with lab/field measurements (Figure III.6). This level of thermal heterogeneity was much reduced when the model was used to simulate the same leaves but with no microtopography (i.e., perfectly flat leaves). Our study was the first to pinpoint the key role of leaf surface microtopography in generating this thermal heterogeneity at the surface of tree leaves. Moreover, we highlighted that previous studies underestimated this within-leaf thermal heterogeneity because the measurements were done under low radiation levels, corresponding to leaves in the shade. Therefore, single leaves of about 20 cm<sup>2</sup> could offer a broad thermal mosaic to arthropods living at their surface.

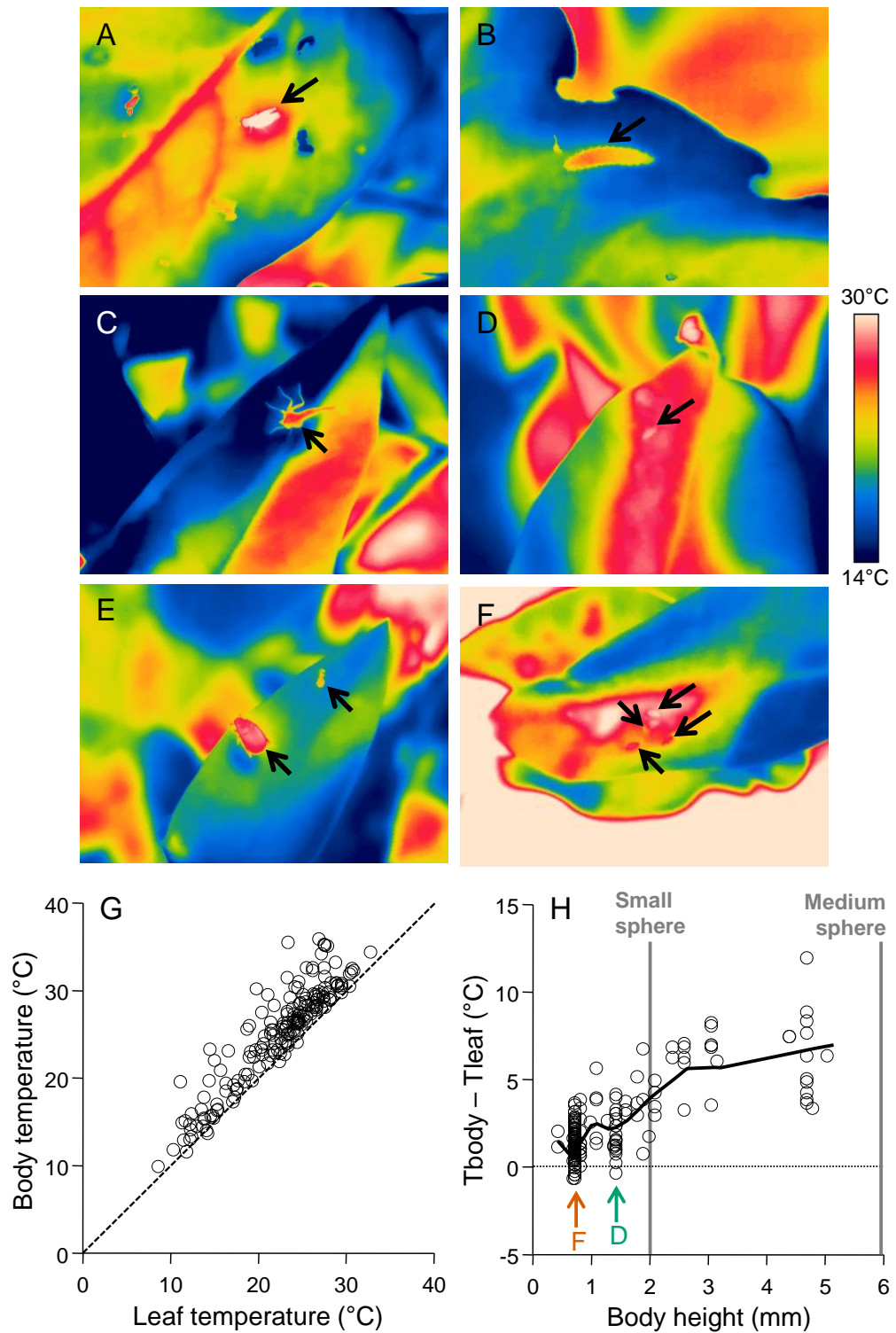


**Figure III.6.** The within-leaf heterogeneity of surface temperature. The graph shows a comparison between the surface temperature distributions of a single apple leaf when measured with a thermal camera under controlled conditions (blue) versus simulated with our biophysical model at a high radiation level. The red triangle on the x-axis indicates air temperature. The images on the right illustrate the thermal image (bottom) and the model output representation (top). The set of images at the top of the figure illustrates the 3D mesh of a single leaf after it was scanned and cleaned, and another comparison of a model simulation (top right) and a thermal image taken in the field. While the model can over-estimate the hottest temperatures at the individual leaf level, it performs reasonably well on average.

The works detailed above deal with leaf surface temperature. Ultimately, the most important variable (for those interested in the ecology of ectotherms) is the body temperature of arthropods living at the leaf surface. We noticed that usually the body temperature of tiny arthropods like spider mites and some aphids (<1 mm in size) is close to the temperature of their surface – something easy to measure with an infrared camera when assuming that the emissivity of the leaf and insect body are near each other: the arthropods are barely visible on the infrared image. Most arthropods are small enough to live in these microclimates at very fine spatial and temporal scales, including the leaf boundary layer. Nevertheless, the body size threshold at which the heat budget of the arthropod becomes less coupled (and at some point decoupled from) to the leaf surface temperature has never been really identified (but see Woods 2013). Recently, I investigated this relationship between insect body size and this coupling between their body temperature and leaf surface temperature (**Pincebourde, Dillon & Woods, in prep**). I collaborated with Prof. Arthur Woods (University of Montana) and Prof. Michael Dillon (University of Wyoming) on a field experiment at the biological station of the University of Wyoming in the Grand Tetons National Park (USA). We combined different methods (thermal imaging, temperature dataloggers with fine thermocouples, and operative temperature models) to test the hypothesis that body temperature varies with body size relative to the leaf boundary layer thickness. Indeed, the heat budget of small organisms living *within* the leaf boundary layer should be driven by conduction and convection mechanisms while the body temperature of organisms popping out of the leaf boundary layer is expected to be largely influenced by radiation load. We found that body size determines the patterns of body temperature (Figure III.7). Larger bodies were warmer than smaller organisms when exposed to solar radiation, and they were all warmer than ambient air. Small ectotherms had a body temperature close to the leaf surface temperature while large insects were systematically warmer than the leaf surface. By contrast, in the shade, all organisms and surfaces had similar temperatures (within 2°C). Interestingly, among the body size metrics, body height was the best explanatory variable (Figure III.7-H). We detected a body size threshold around 2-3mm above which the body temperature becomes less influenced by increasing body size. Above this threshold, body temperature remains roughly 5-8°C warmer than the leaf surface, supposedly because the radiative heat is the main driver of their heat budget. All the organisms we



sampled still had a body temperature coupled to leaf surface temperature. The largest operative temperature model (black spheres of 10mm), however, was clearly decoupled from leaf surface temperature but we did not find arthropods of this size on the leaves we sampled. Small organisms compose a large portion of the biodiversity (May 1988). The mechanisms behind this relationship between body size, body temperature and leaf surface temperature need to be detailed to be further integrated into a biophysical framework on the response to climate change.



**Figure III.7.** Relationship between body size, body temperature and leaf surface temperature in a community of arthropods living on leaves of arrowleaf balsamroot, *Balsamorhiza sagittata*. [A-F] Thermal images showing the body temperature of various species (indicated by arrows); The temperature scale is the same for all images. [G] The body temperature of ectotherms scales with the temperature of the leaf surface near the arthropods, when taken at the community scale. [H] Relationship between the body temperature excess (deviation between leaf surface and body temperatures) and body height. The species shown in [F] and [D] are indicated on this graph.

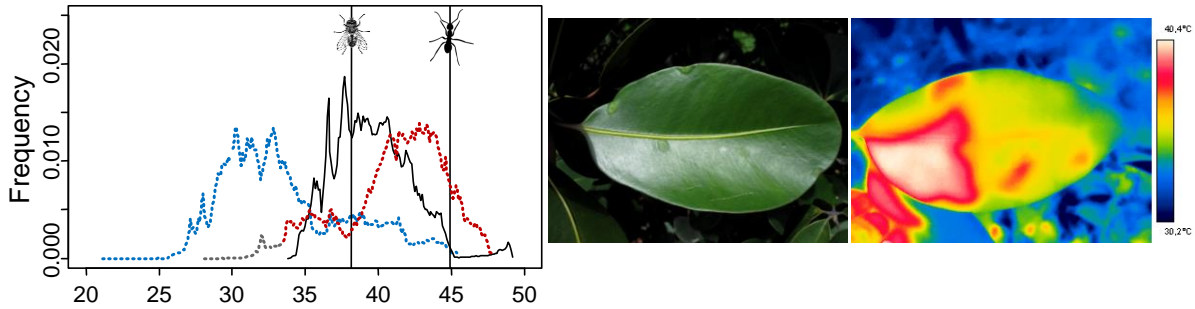
The different paragraphs above deal with leaf temperature at various spatial scales from a latitudinal gradient down to the within-leaf surface thermal range. Therefore, we are now in the position to compare the level of thermal variance across the different spatial scales that matter for arthropods living at the surface of leaves. The comparison is less straightforward than it seems however because the methods used to measure leaf temperatures are not the same in the different studies. Direct measurements with thermocouples were made for the study on latitudinal gradient of leaf temperature while thermal imaging was used to record the within-leaf surface heterogeneity. With this in mind, we ranked the levels of thermal variance and found that the temperature gradient is higher at the within-leaf surfaces exposed to full sun compared to across a single canopy and across a latitudinal gradient (**Pincebourde et al. in prep**). Basically, a small arthropod like a spider mite can sample as much degrees Celsius when moving across a single leaf in full sun (few cm) than a theoretical spider mite that would 'fly' from the South of France up to Belgium (almost 1,000 km). This comparison raises exciting questions about how we should think conceptually about the potential impacts of climate change on organisms living in microclimates.

Then, I decided to measure directly in the field, using the same methodology (thermal imaging), the level of thermal variance of the leaf microclimate at different spatial scales from the scale of a single leaf up to the scale of the landscape (**Pincebourde & Suppo 2016**). I studied the microclimatic diversity at the top of an Inselberg in a tropical rain forest of South America. Inselbergs are isolated mountains, often granitic, emerging out of the forest in humid forests of South America (Sarhou et al. 2003). The climate of Inselbergs is generally warmer and less humid than within the canopy layer of surrounding primary forests, and they are often described as harsh habitats (Burke 2003). Thermal imaging was used to quantify the heterogeneity in surface temperature at the scales of a landscape, a single shrub, and a single leaf on an Inselberg in French Guyana (Figure III.8). We measured the thermal heterogeneity at the scale of *Clusia nemorosa* leaves (in the sun versus in the shade). Then, I measured the thermal heterogeneity at the scale of a single *Clusia* shrub and the landscape, for several sites differing in their orientation toward the sun. The thermal variance varied between scales, increasing from the within-leaf surface to the landscape scale supporting the conclusion above on apple leaves. Thermal variance also shifted across the day in different ways depending on

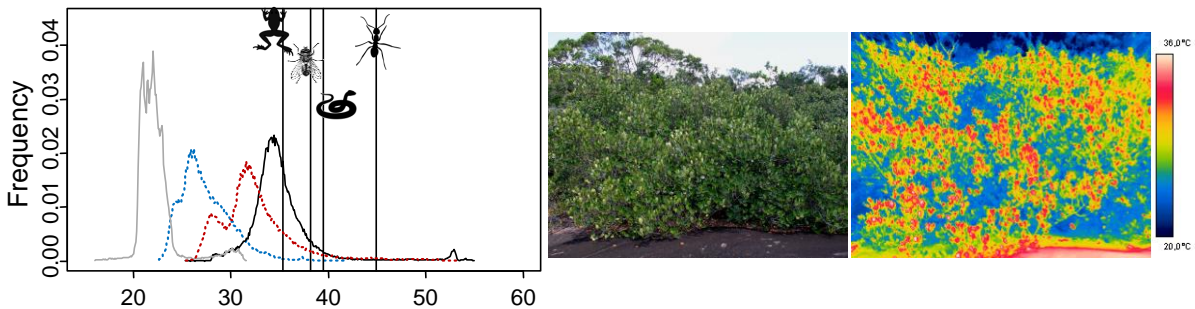
the spatial scale. Overall, temperature ranges of an order  $>10^{\circ}\text{C}$  was recorded at all spatial scales, which provided significant safety margin for ectotherms in general (Figure III.8). Later, we enlarged this comparison by compiling data on temperature ranges measured at various spatial scales for various ecosystems (plant and intertidal surfaces) and ranked them as landscape, local and micro-scale (Pincebourde et al. 2016). This preliminary analysis showed that the temperature range does not clearly change across spatial scales. This result contrasts with our empirical study above on plant surfaces, indicating that the level of thermal variance across spatial scales mostly depends on the ecosystem.



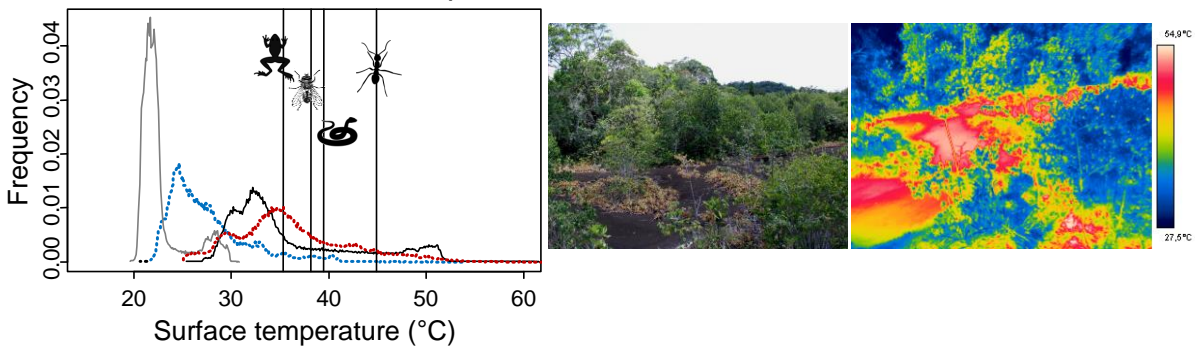
A. Sunny leaves



B. South oriented shrubs



C. South oriented landscapes



**Figure III.8.** Distribution of plant surface temperatures at the scale of (A) a single *Clusia* leaf, (B) a single *Clusia* shrub, and (C) a landscape at the top of an inselberg. The temperature distributions are shown for morning (blue), midday (black) and afternoon (red). The grey distributions are for nighttime. Vertical lines indicate the CTmax of tropical ectotherms (amphibians, insects excluding ants, reptiles and ants). The photographs at the top illustrates views of an Inselberg in French Guiana. Photographs on the right are the visible and infrared images taken at the corresponding scale.



Few ecosystems are recognized for the high level of thermal variance at small scale. The rocky intertidal ecosystem is interesting to explore the spatial scale at which most thermal variability occurs (see *Part II: Overview of the field*). Here, the microclimate is generated mostly by an abiotic object (the rocky shore splashed by sea water). We followed the body temperature of an intertidal invertebrate at low tide (ochre sea star *Pisaster ochraceus*) in the field during an entire year as function of its position along the intertidal elevation gradient as well as its use of refuges from solar radiation. Biomimetic loggers were deployed on the rocky shore within the distribution range of the species and the positions of live sea stars during low tide were recorded relative to the location of the loggers. Integrating data on tidal elevation of sea star, microhabitat and body temperature indicated a seasonal variation in aerial body temperature patterns (Pincebourde et al. 2008). This seasonal pattern was driven by the location high on the shore of the mussel bed (prey) and by the characteristics of the tide cycle at the study site, which exposes ectotherms to air at low tide during midday only in spring. Overall, we found that the body temperature of sea stars varies by more than 15°C potentially along the intertidal gradient at the scale of a distance of only 20 m. As for the leaf microclimate, solar radiation is the main driving force of sea star body temperature, coupled with sea water temperature which ‘splashes’ and cool down the sea stars when they are positioned low enough in the intertidal.

By contrast, other ecosystems are thought to have a low thermal variance at small scale. The water temperature of lentic freshwater ecosystems (e.g., ponds) is often supposed to be much less variable than the temperature of terrestrial microclimates. Thus, macroinvertebrates should experience thermal variations of lower amplitude than in the atmosphere. However, the spatial heterogeneity of water temperature within a pond is rarely though to be significant enough to offer ectotherms a temperature choice (Dallas & Rivers-Moore 2011). We quantified the differences in water temperature along three axes within selected ponds of different geomorphological structure: (i) among different microhabitats close to the pond bank and at a standard depth, (ii) along a depth gradient at the surface of the pond substrate (from the bank toward the middle of the pond), and (iii) along a depth gradient in free water (middle of the pond). These microhabitats are used by various Odonate larvae. We deployed dataloggers that were set to measure water temperature at a high temporal resolution. Water temperature fluctuated daily by buffering

maximal aerial temperatures, as expected. We found that water temperature differs on average by up to 3°C among different locations near the bank within ponds, mostly due to differences in vegetation and shade. Extreme water temperature values differed by as much as 5°C among different location separated by less than 50m within a large pond. In addition, water temperature at the surface of the substrate varies by up to 10°C between a depth of 10 cm and 70 cm. In general, the surface of the substrate remains cooler by few degrees than the free water at a similar depth (**Pincebourde et al. in prep**). Therefore, ponds also show some levels of thermal heterogeneity in space, which can be exploited by macro-invertebrates.

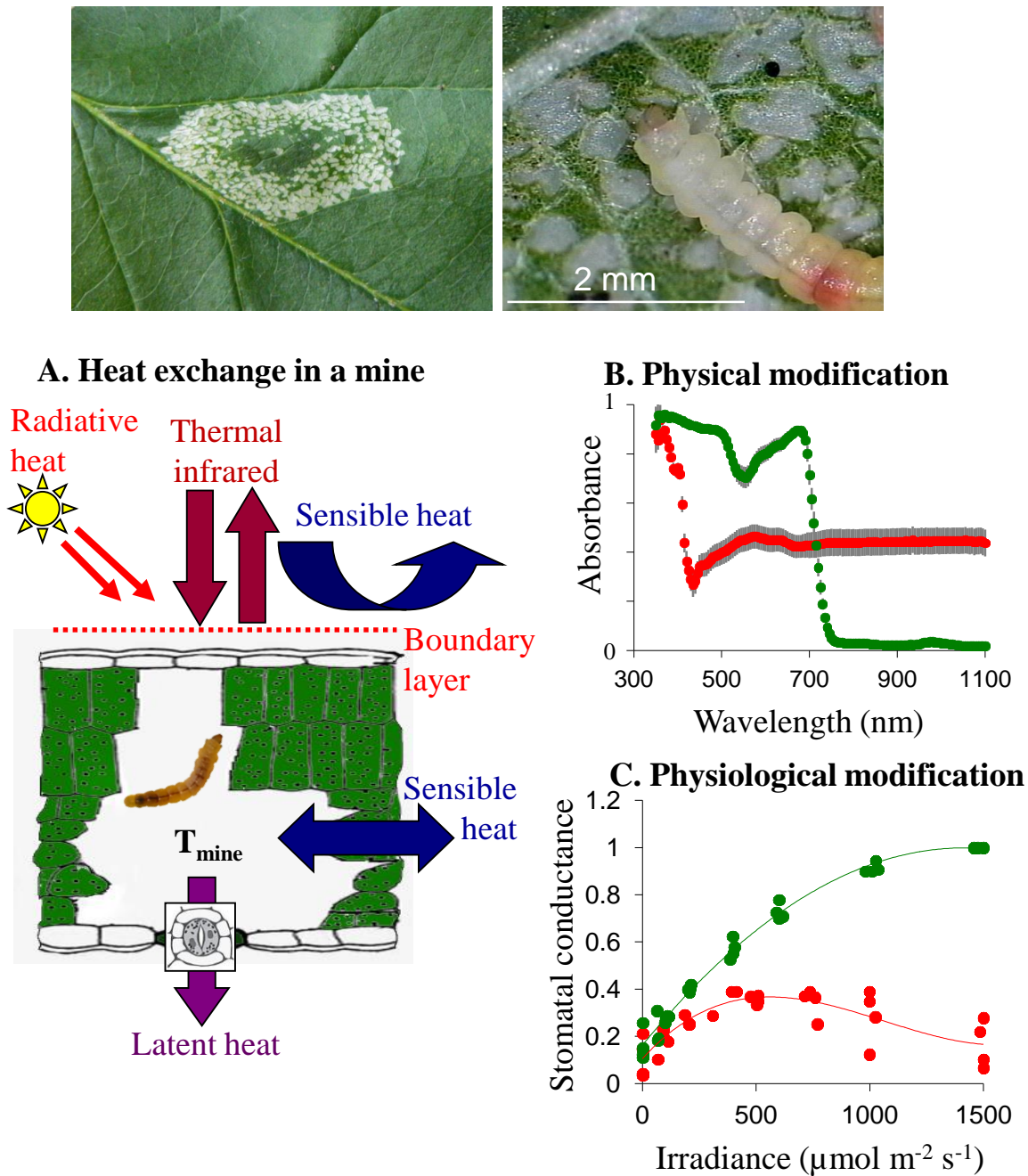
*Conclusion* - 'There is plenty of room at the bottom' (Feynman 1959, in Casas & De Salvo 2018). This sentence makes a lot of sense in the context of microclimate diversity: there is plenty of microclimate diversity at the smallest spatial scales, and perhaps even more at small than at large scales for some ecosystems. This idea is not totally new – ecologists working on behavioral thermoregulation know well since long that moving over short distances can make a difference for body temperatures. For some reasons however, current approaches in global change ecology do not integrate this possibility into impact models. This inclusion is likely not straightforward but I see this as the next stepping-stone for the field of global change biology.

*b) Ectotherms modulate their microclimates*

Objects in the environment create microclimatic temperature conditions that deviate from the temperature of the surrounding air. Nevertheless, organisms can induce changes in the properties of these objects to achieve novel microclimates. The best example of such modulation of the microclimate is the termite mound (Turner 2000). During my research, we illustrated this effect with the object being another living organism (plant tissues), with the apple leaf miner *Phyllonorycter blancardella* (Lepidoptera: Gracillariidae). The caterpillar of this microlepidoptera develops within the apple leaf tissues, inside a structure called a mine (Figure III.9). During its development, the insect modifies different properties of the plant tissues. At the last larval instar (L5), the optical properties of the mine surface differ from those of intact leaf tissues and the mine absorbs more near-infrared radiations (**Pincebourde & Casas 2006b**). Also, the stomata in the (lower) L5 mine integument remain



functional and their behavior changes compared to stomata in intact leaf tissues, causing stomatal closure at high irradiance (**Pincebourde et al. 2006**). A biophysical modeling approach showed that these physical and physiological modifications of the leaf tissues by the caterpillar are contributing to retention of energy within the mine, resulting in a mine atmosphere being warmer than both the intact leaf surface and the ambient air (**Pincebourde & Casas 2006a**). While the maximal temperature excess in the mine was around 8°C in the field (**Pincebourde et al. 2007**), the biophysical model indicated that mine temperature can be up to 12°C warmer than ambient air during extreme (but realistic) atmospheric conditions with low wind speed and high radiation level (**Pincebourde & Casas 2006a**). This temperature excess applies to the mine of the last larval stage (L5). The physical and physiological changes of the leaf tissues are however occurring gradually across the ontogeny of the caterpillar (**Pincebourde & Casas 2015**). The egg and the first three larval stages do not modify the parameters linked to the heat budget of a mine, and therefore they experience the temperature of an intact leaf surface. The ‘true’ structure of a mine starts to be visible at the fourth larval stage: modifications are moderate and the temperature of a mine starts to deviate from the leaf surface. Then, the fifth larval stage provides the most striking modification leading to the maximal temperature excess observed in mine at the end of this stage and during the nymph stage. These ontogenic modifications and related temperature shifts are occurring at the scale of a single mine, i.e. about 1cm<sup>2</sup> of leaf area.

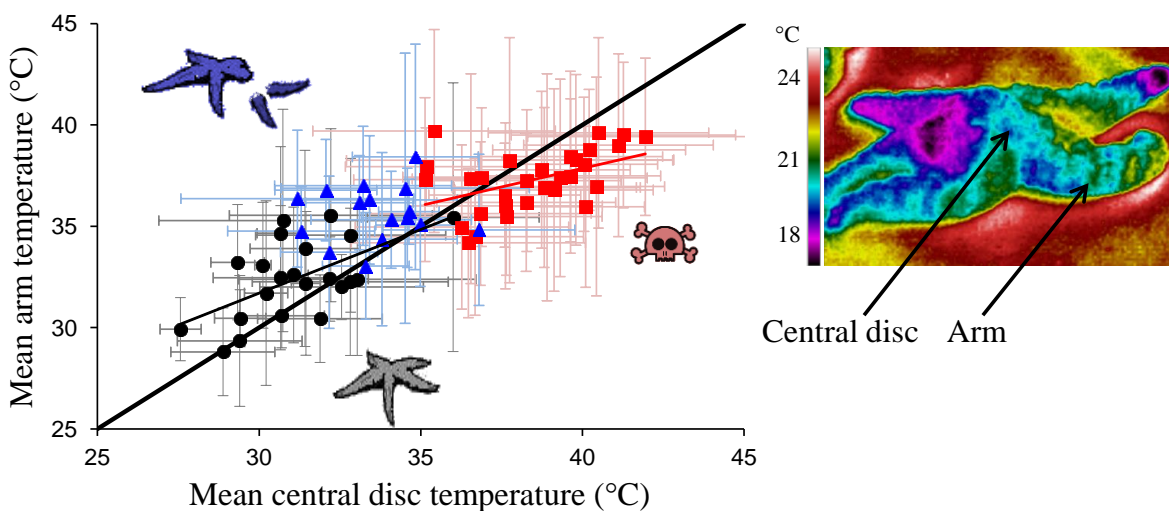


**Figure III.9.** The biophysical functioning of a leaf mine (*P. blancardella* on apple). The photographs at the top shows the mine surface from above ( $\sim 1\text{cm}^2$  area) and the inside of a mine once one opens it, with the larva and the feeding windows (white patches where only the leaf integument remains after the larva fed on the chlorophyll-containing tissues). (A) A diagram illustrating the various heat exchange mechanisms between the mine, the environment and the adjacent leaf tissues. (B) The physical modification of the leaf tissues induced by the larva: absorbance of mine integument as function of wavelength (green: intact leaf tissues; red: mine integument) showing the high absorbance of near infrared energy in the mine. (C) The physiological modification: stomatal conductance of the mine integument as function of irradiance (green: intact leaf tissues; red: mine integument), showing the stomatal closure in the mine.

The leaf miner system is particular because the insect profoundly changes the plant tissue properties by living within them. We asked the question if a similar process could also be observed with insects feeding externally from the surface of the leaf. Insect herbivores induce changes in plant gas exchange when feeding on leaf tissues (Welter 1989). From a biophysical point of view, a change in stomatal behavior causes a variation in plant transpiration rate. Therefore, we tested the hypothesis that herbivores causing a lower leaf transpiration rate experience a warmer leaf surface compared to insects that induce higher transpiration rate. To test this hypothesis and to limit the potential effects of covariables and independent factors, we measured leaf gas exchange during herbivore feeding on a community of species with the following criteria. These species should be living at the surface of the same host plant to avoid different ecophysiological responses of different host plants. They should have small body size to ensure that they are all embedded within the leaf boundary layer (their body temperature equals surface temperature). The species differed in their feeding guild to maximize the range of the effects of the community on leaf transpiration rate. This careful design allowed us to show that herbivores (e.g., spider mites) live on warmer surfaces when they decrease leaf transpiration rate, while they (e.g., aphids) experience cooler surfaces as they increase leaf transpiration rate. The maximal surface temperature experienced by spider mites is up to 9°C higher than for aphids (**Pincebourde & Casas 2019**). Therefore, ectotherms can modulate the temperature of their own microclimate in very subtle ways. Such species can be listed as ecosystem engineers.

Organisms can modulate their own properties to adjust their body temperature. These mechanisms of thermoregulation are well covered in the literature (e.g., Stevenson 1985). During my postdoctoral studies, in collaboration with Prof. Brian Helmuth and Prof. Eric Sanford, we discovered a novel thermoregulation strategy in an ectotherm. The ochre sea star (*Pisaster ochraceus*) can be exposed to solar radiation on rocky shore at low tide. The sea star cannot move when it is exposed to air, and displacements are constrained by the high tide duration. We designed an experiment with water tanks, sea water flowing in continuously and simulated tide cycle to control for both sea water temperature and sea star body temperature when exposed to air at low tide (**Pincebourde et al. 2009**). During 10 days, sea stars were exposed to stressful aerial conditions (high air temperature) and we followed their wet body mass. We found that when the sea star

experiences thermal stress during a low tide, it accumulates more sea water into its body cavity during the following high tide to be prepared for the next low tide with probable thermal stress. This increase in wet body mass results in a clear increase in thermal inertia of the body, delaying thereby the moment at which the sea star reaches its maximal aerial body temperature. At some point, the low tide period is shorter than the thermal inertia and aerial body temperature at the end of a low tide decreases. This strategy works well for a large ectotherm such as this sea star with a body mass of 200-400g, but it is unlikely for tiny ectotherms. The ochre sea star really is a 'thermal warrior'. The body of the sea star has regional heterothermy: the central disc is cooler than the arms (Figure III.10). We discovered further that this sea star loses one to 3 arms (it has 5) after exposure to extreme high aerial body temperatures (Pincebourde et al. 2013). The arm(s) that was detached by autotomy was indeed the warmest arm during exposure to high aerial temperature. Our study suggests a dynamic system of heat/fluid circulation within the body of the sea star allowing it to derive most of the heat from the central disc (where vital organs are) to one or several arms, which will be sacrificed in the end. The ochre sea star is an iconic organism on the West coast of the US, and it has been studied for long especially since the studies of Paine (1966). Our studies, connected with the research from other teams (Menge et al. 2011), indicate that this sea star is not necessarily challenged directly by warming (in both the air and the water). Instead, warming is promoting a disease (virus) that is able to clear entirely populations (Menge et al. 2016).



**Figure III.10.** Mean ( $\pm$ s.d.) arm temperature as a function of mean ( $\pm$ s.d.) central disc temperature in *Pisaster ochraceus*, including the survivors with intact arms (black circles) and arm abscission (blue

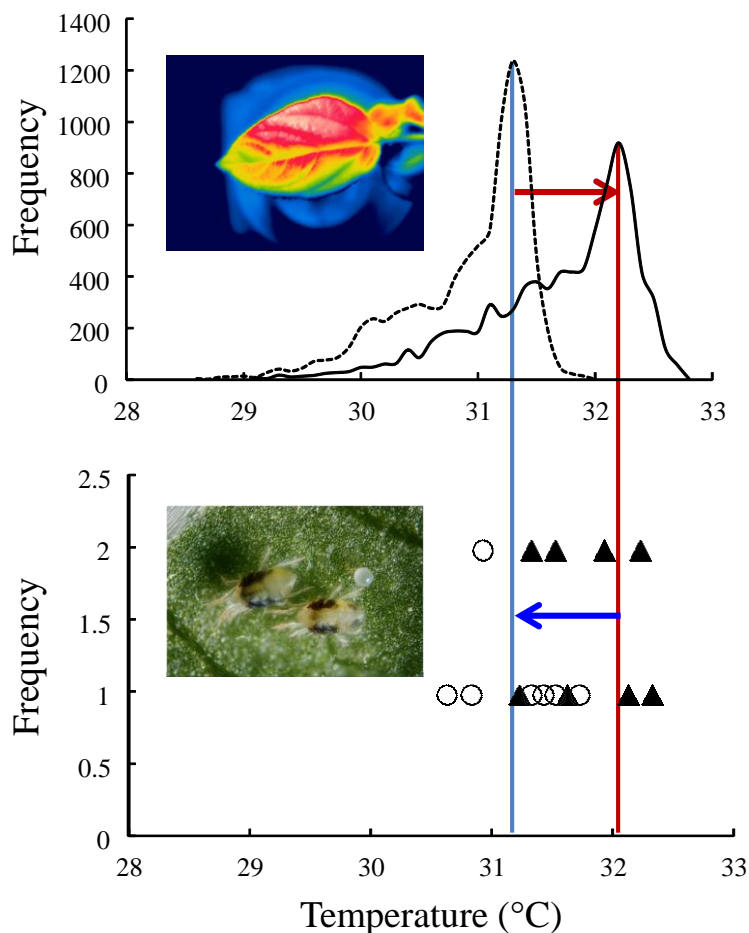
triangles), as well as the individuals that died (red squares). The linear regression lines are shown when correlations are significant. The black line indicates the equality of the two variables. The inset is an infrared image of a sea star during the exposure to experimental heating, illustrating the thermal heterogeneity of the sea star body surface (the color scale indicates temperature range).

**Conclusion** - Our set of studies shows that there is still much to discover on thermoregulation strategies even on model organisms, despite early syntheses such as the book 'Thermal Warriors' of Bernd Heinrich (1996). The modulation of microclimates can be seen as a strategy to thermoregulate and it often involves both physiological and behavioral processes. The potential impacts of climate change on such strategies remain underexplored.

*c) Ectotherms exploit this diversity behaviorally*

Behavioral thermoregulation is a classical way of dealing with the local spatial heterogeneity of temperature to avoid overheating and/or to perform at or near the optimal temperature for physiological processes. Although behavioral thermoregulation is largely documented in insects (May 1979), the extent to which they use the thermal heterogeneity at the surface of a single leaf was never studied before. We started to work on a spider mite (*Tetranychus urticae*) on apple leaves during the early infestation process when the leaf is not severely attacked yet. With my PhD student Robin Caillon, we designed an experiment involving two cameras: a digital camera positioned below the leaf was used to follow the movement of spider mites underneath the leaf while an infrared camera was recording leaf surface temperature patterns from above (Caillon, Suppo, Casas, Woods & Pincebourde 2014). Indeed, the apple leaf is thin enough such that both sides show similar temperatures (within 0.5°C). The setup was placed inside a climatic chamber to manipulate the environmental conditions (e.g., moderate versus hot air). Our hypothesis was that the within-leaf thermal heterogeneity should allow the spider mites to escape overheating under challenging environmental conditions with hot air and high radiation level. Our results did not support this expectation. Surprisingly, the leaf surface thermal mosaic is more homogenous under hot air than under moderate conditions. Therefore, the spider mites cannot find a 'thermal refuge' at the leaf surface under challenging conditions. We suppose that this spider mite should have evolved physiological mechanisms to deal with extreme high temperature,

explaining thereby the high thermal limit in this species (upper lethal temperature 46°C). However, another surprise came under moderate environmental conditions corresponding initially to our control groups. The within-leaf thermal heterogeneity was maximal under radiation when air temperature was around 30°C. The spider mite was observed to move and use the leaf patches that were close to 31°C, which corresponds to the optimal temperature for larval development in this species (Figure III.11). This result indicates that *T. urticae* thermoregulates behaviorally to find its optimal temperature for development. Our study illustrates that information on spatial variance of microclimatic conditions is critical for estimating how readily organisms can buffer global warming by moving.



**Figure III.11.** Frequency distributions of leaf surface temperatures and spider mite position at the leaf surface. White circles show the spider mite temperature during the leaf temperature distribution indicated as dotted line, while black triangles correspond to the temperature distribution shown by the black line. The blue and red lines indicate the median of the distributions. This example shows how the spider mite body temperature distribution shifts towards cooler temperatures when leaf surface distribution increases towards higher temperatures.

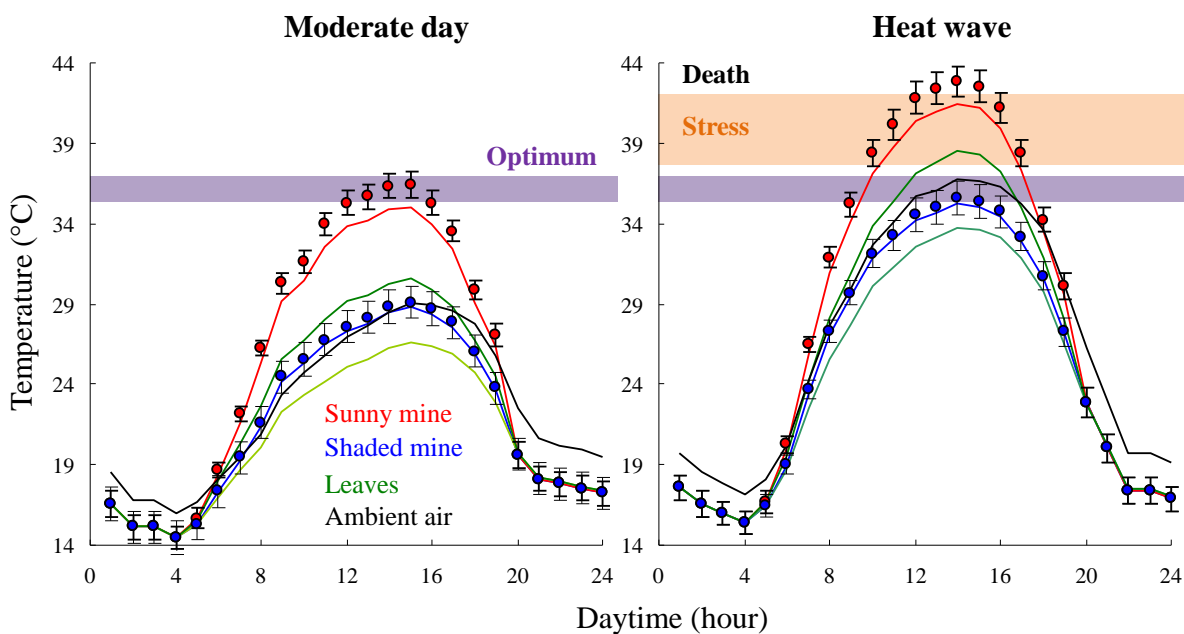


Following this study above, we wondered to what extent this conclusion applies to other herbivore arthropods. In particular, spider mites are able to feed on plant tissues from anywhere at the leaf surface. By contrast, most aphid species have to be near or on the veins to feed on the phloem. This feeding imperative may constrain the thermoregulation behavior. Therefore, we used the same experimental design with two cameras (digital and infrared) to record simultaneously the movements of the green apple aphid *Aphis pomi* and the leaf surface temperature (Cahon, Caillon & Pincebourde 2018). Again, we did this study at the stage of early infestation, before aphids induce much change in the leaf ecophysiology. As expected we found that the aphids are not moving at the leaf surface to exploit the leaf thermal mosaic. Instead, they remain near the main and secondary veins to feed on the phloem. Consequently, these aphids are living at the warmest spot at the leaf surface, which was few degrees above mean leaf temperature. These aphids may therefore experience environmental warming in a slightly different way than the spider mites above. Aphids should be exposed more systematically to extreme surface temperatures while spider mites are still able to change slightly their position at the leaf surface, even though this move induces a change of only 1-2 degrees in body temperature. But even a small temperature change makes a difference when temperature approached thermal limits.

These two examples above are focusing at the leaf scale. The scale of a single tree canopy also offers plenty of microclimate diversity to potentially exploit. In the leaf miner field study (Pincebourde et al. 2007) we simulated the microclimate temperature (i.e., temperature within a leaf mine of *P. blancardella*) across an apple tree canopy with a strong temperature gradient. We simulated two types of atmospheric conditions with (i) typical (moderate) summer conditions for the area of Tours versus (ii) conditions during the extreme heat wave we had in 2003 in Europe (note that this heat wave was considered extreme at that time but the atmospheric temperature was 5°C degrees below the heat waves we got recently in 2019). The results indicated that mines on leaves exposed to solar radiation provide the optimal thermal environment for the development of the caterpillar during the typical summer conditions while caterpillars mining leaves in the shade are at suboptimal temperature (Figure III.12). By contrast, during the heat wave, leaf mines in the sun are dangerously overheating leading to mortality and the optimal temperature was reached in mine in the shade (Figure III.12). The integration of the thermal

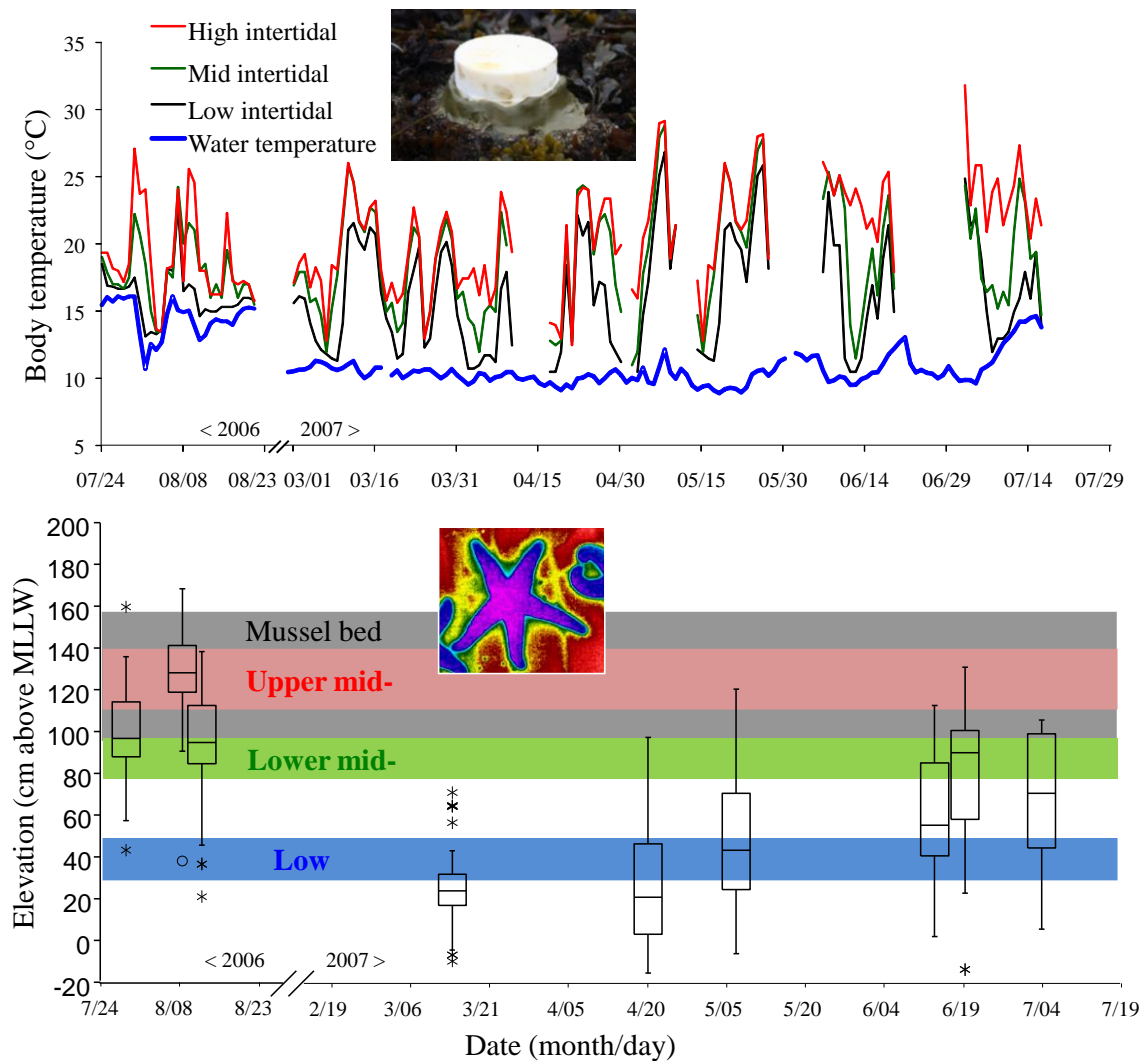


performance curve for development rate explained to fast decrease in sunny mine quality under extreme heat. These results provided an explanation to the behavior of the female which lay eggs everywhere within a tree canopy. The shifting mosaic of favorable and unfavorable thermal environment makes impossible to predict where will be the best place to lay eggs. Like for most leaf miner species, a slow development rate mean a higher probability to get attacked by a parasitoid. In this context, it is better for the female to lay eggs everywhere to ensure that at least part of the clutch will contribute to the next generation in this sessile insect.



**Figure III.12.** Integrated biophysical model predictions of leaf and mine temperatures at shaded and sunny locations for the moderate day (left) and the hot day taken during heat wave conditions (right). Mean ( $\pm$  SD) body temperature of larvae within mines is also shown (circles). The orange zone indicates the temperature range inducing heat stress. Temperatures above the stressful range are lethal (at an exposure of 1 h). The purple area indicates the optimal temperature for larval development. Legends: lines are surface temperatures for leaves in the shade (pale green) and the sun (dark green), air temperature (black), and mines in the shade (blue) and the sun (red): circles show body temperatures for larvae in sunny mines (red) and shaded mines (blue).

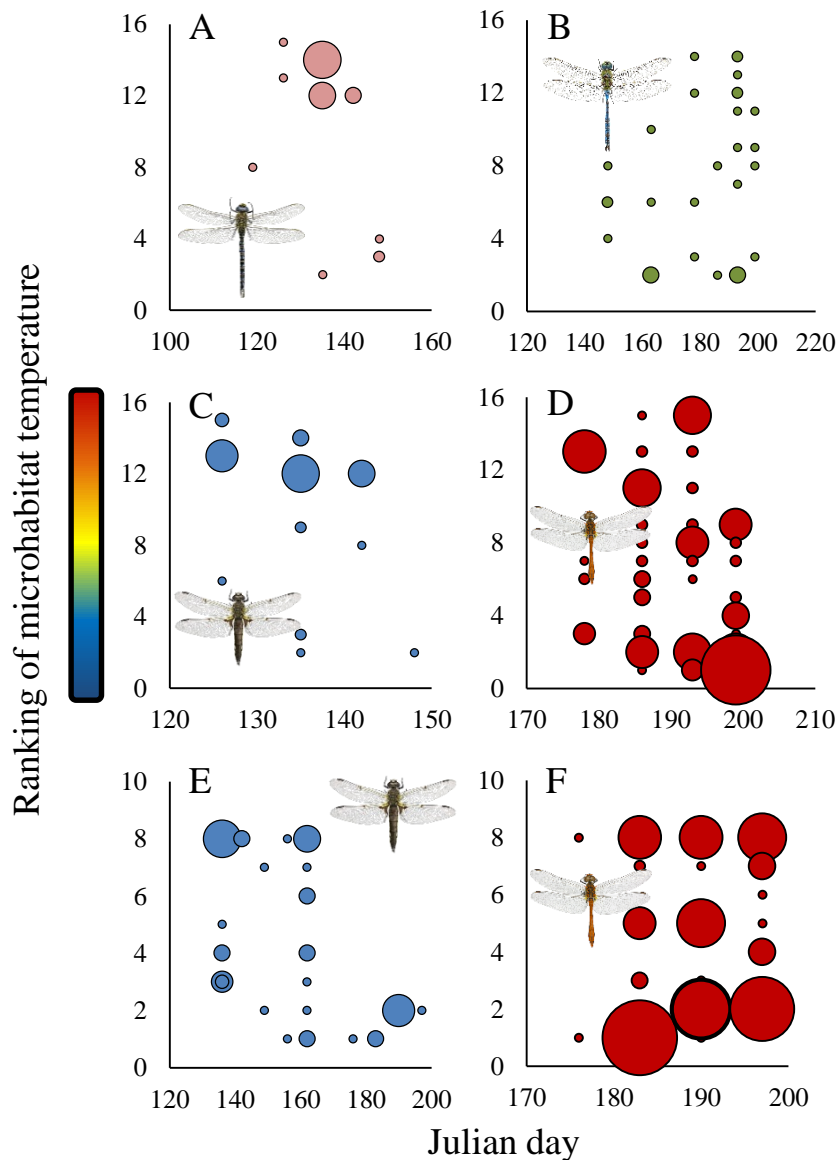
The rocky intertidal habitat provides a level of thermal heterogeneity of the same order of a tree canopy when both are appropriately scaled for comparison. The shade/sun exposure gradient within a tree canopy compares well with the intertidal elevation gradient. The work I did on the microhabitat uses by the sea star *Pisaster ochraceus* indicated a clear seasonal pattern in the position of the sea star at low tide along the intertidal elevation gradient (Pincebourde et al. 2008). The pattern was strongly linked to the tide cycle which exposes animals to midday solar radiation only at a given period of the year in April/May. Consequently, sea stars foraged mostly in the low intertidal during spring and early summer and they move upper in the intertidal from summer to fall (Figure III.13). Sea stars also used more frequently refuges such as crevices and cracks in the rock in spring than in summer. Only the conditions in the summer allowed these sea stars to remain near their mussel prey (Figure III.13). Sea stars in the field frequently experienced body temperatures above 23°C for short periods of time (3–4 d) (Figure III.13), and the laboratory trials indicated that these conditions increase sea star performance in opposition to chronic exposure to such temperatures. The negative effects of chronic exposure were detected at body temperatures above 23°C, suggesting that 23°C is the threshold inducing thermal stress in this species. The sea stars somehow manage to compensate for thermal stress when it happens during less than four consecutive days. This study (Pincebourde et al. 2008) was indeed the very first to report the shift in microhabitat use across the year in this iconic species.



**Figure III.13.** (Top chart) Daily mean aerial body temperatures, as recorded by biomimetic data loggers (inset: picture of it) in low (black line), mid (green line), and upper intertidal (red line) during summer 2006 and spring and summer 2007 (SD eliminated for clarity). Sea water temperature is shown in blue. (Bottom chart) Monthly intertidal elevation patterns of *P. ochraceus* populations (box plot charts). In each box plot, center horizontal line marks median of sample. Length of each box indicates range within which central 50% of the values fall, with box edges at first and third quartiles. Whiskers: range of values that fall within inner fences. Asterisks: values within inner and outer fences. Empty circles: far outside values. The gray zone indicates mean elevation of mussel bed in the area. The mean elevation of biomimetic data loggers for both 2006 and 2007 are indicated by the color areas: low (blue), mid (green) and upper intertidal (red).

The section above on microclimatic diversity shows that the lentic freshwater ecosystem has less thermal variability than the rocky intertidal and the plant environments. It is still significant and we have unpublished data suggesting that dragonfly larvae might indeed exploit the within-pond horizontal variability in water

temperature (**Pincebourde, Muller, Casas, Sansault & Baeta in prep**). As we measured water temperature at a standard depth across several spots around several ponds (see above), we also collected the exuviae of dragonflies around each datalogger every week. Exuviae were used as a proxy for emergence success and microhabitat use of the last larval stage. Then, we related the maximal water temperature during previous week of exuviae collection and the number of exuviae collected for each spot, each dragonfly species and each of four ponds. We found various patterns depending on the species. Time strongly constrains the phenology of dragonflies (Hassall 2013). Spring species emerge only early in the season. We observed that these species were mostly emerging at the warmest spots around a pond (Figure III.14-A, C). One of these species had a longer phenology in one of the ponds, and it was observed to emerge exclusively at the coolest spots later in the season (Figure III.14-E). By contrast, summer species that emerge only later during the season were found almost at all spots with a statistically unclear tendency to emerge more at the coolest spots around the pond (Figure III.14-D, F). Finally, some species have a much boarder phenology and they emerged both in spring and summer periods. No clear pattern was found in these species in relation to water temperature (Figure III.14-B). This study shows that spring species emerge more in the warmest spots of the ponds when ambient temperature is still cool, while summer species may prefer to finish their development at the coolest spots when ambient air is hot. There are two hypotheses to explain these patterns. Larvae may exploit the spatial heterogeneity in water temperature within the pond to select a suitable thermal environment when finishing their development. Alternatively, the water temperature modulates the rate of development of the larvae such that the phenology of species is extended. The variety of patterns across species may indicate that the two hypotheses hold in species-specific way.



**Figure III.14.** Relationship between within-pond spatial heterogeneity in water temperature and number of dragonfly exuviae retrieved each week at several spots around ponds across the season. The different spots around the pond were ranked from the coolest (rank#1) to the warmest (rank#15 or 8 for the 2 sites respectively). Sites: [A to D] Givry; [E, F] Les Landes Vendues. Species: [A] *Brachytron pretense*; [B] *Anax imperator*; [C, E] *Libellula quadrimaculata*; [D, F] *Sympetrum sanguineum*. The size of the data points (filled circles) is proportional to the number of exuviae. The circle with a thick border in [F] should actually be 2-fold larger in size (it was reduced for clarity).

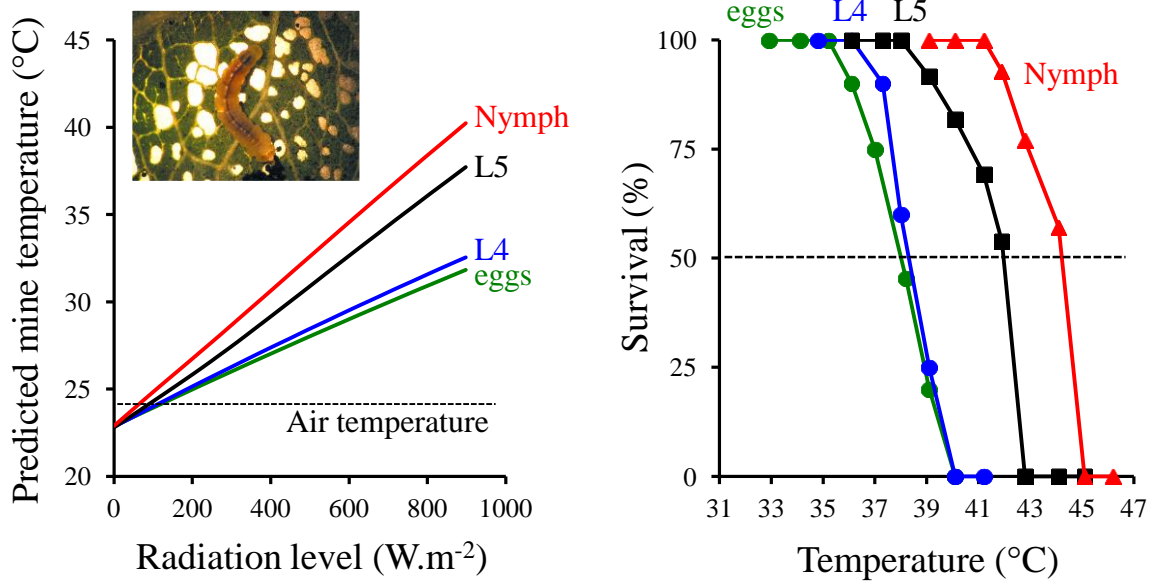
**Conclusion** - The degree to which ectotherms exploit the environmental heterogeneity during thermoregulation obviously varies between species, but not among ecosystems (plant covers vs. rocky intertidal vs. freshwater). This suggests that the ability to adapt to environmental changes will vary accordingly since it is

well documented now that behavioral thermoregulation is limiting the ability to respond plastically and further to adapt to these changes.

*d) Adaptations to microclimatic conditions*

Part of my research asked to what extent microclimatic conditions impose selective pressures on ectotherms. Several studies already showed that ectotherms (in particular reptiles and amphibians) are specifically adapted to the thermal conditions they experience in their microhabitat (Navas 1997; Labra et al. 2009). But these studies operate at a rather coarse spatial scale. My objective is to show that microclimatic temperature changes at *very fine scale* also drive thermal adaptations in ectotherms. The tree leaf microhabitat is a remarkable biological model to reach this objective.

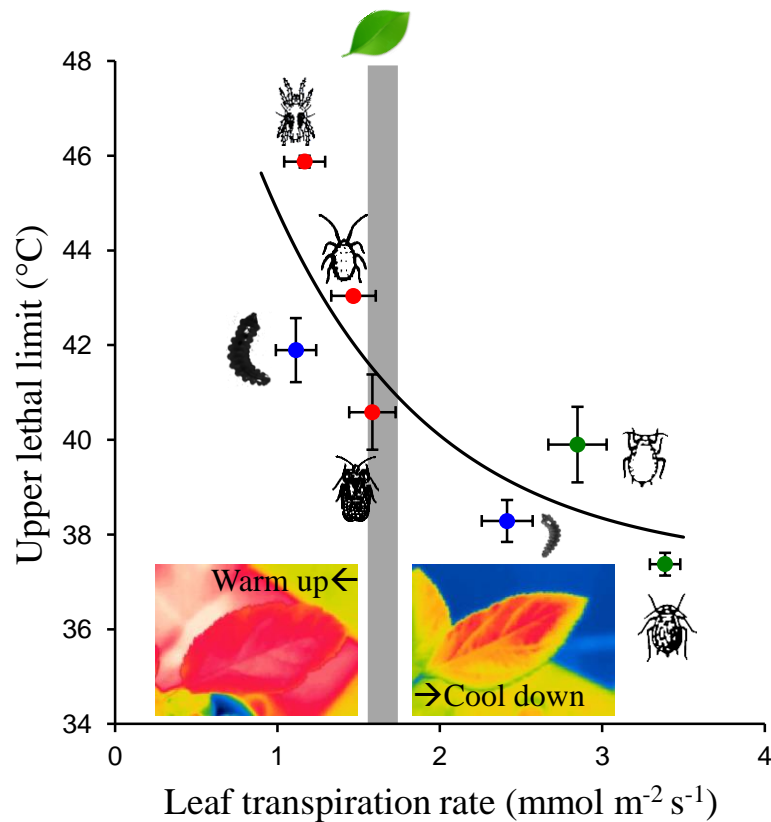
We studied the thermal adaptation of the apple leaf miner *P. blancardella* as function of the temperature within the leaf mine. Across the ontogeny of this species, from the egg to the last larval instar and nymph stage, the biophysical modeling approach indicated that the temperature within the mine increases progressively (when under exactly the same environmental conditions). We measured the thermal limit of each development stage to test if it shifts across ontogeny at the same rate than maximal microclimatic temperature (Pincebourde & Casas 2015). We found indeed that in this leaf miner the older, the warmer and the more tolerant. The thermal limit increases across larval stages at about the same rate (upper lethal temperature  $+7^{\circ}\text{C}$  from egg to nymphs) than the mine temperature change ( $+8^{\circ}\text{C}$  from egg to nymph) (Figure III.15). Therefore, the thermal biology of the leaf miner is well adjusted to the progressive shift in microclimate temperature across the ontogeny. This is a nice example of a species that modifies its microenvironment, thereby inducing changes in its microclimate temperature and causing a feedback effect on its own thermal adaptations. This study (Pincebourde & Casas 2015) was the first 'proof of concept' of such feedback effect in an arthropod herbivore.



**Figure III.15.** (Left chart) Microclimate shift as function of radiation level at the leaf surface and at ambient air temperature 25°C (represented by the dotted line) across the leaf miner life cycle from egg to nymph stage. (Right chart) The shift in thermal limits across ontogeny. Survival rate is shown as function of experienced temperature for each life stage: eggs (circles), L4 (crosses), L5 (squares), and pupae (triangles). The horizontal dashed line represents a 50% survival threshold (considered to be the upper lethal threshold).

We aimed at generalizing this proof of concept to herbivores feeding externally on leaf tissues. The leaf miner system is indeed particular in the sense that it lives inside the plant tissues and it induces several important local changes in the properties of the leaf tissues. We applied the same concept to tiny arthropods feeding at the leaf surface including aphids, spider mites and lace bugs (Pincebourde & Casas 2019). The rationale is that species inducing an increase in leaf transpiration rate also cause the leaf to cool down and should therefore have evolved lower thermal limits than other species that increase leaf transpiration and warm up the leaf surface. In a community of six arthropod herbivores feeding on apple leaves, we collected data supporting this hypothesis (Figure III.16). Each species is specifically thermally adapted to the thermal conditions it induces at the leaf surface, with an upper lethal temperature range of about 8°C between the two extreme species (the two-spotted spider mite versus the rosy apple aphid). This study proposes a great unifying explanation and framework for fine-scale variation in thermal limits in arthropods inhabiting the phyllosphere.





**Figure III.16.** Relationship between the thermal limit of six herbivore arthropods and their respective influence on the leaf transpiration rate (mean±se). The grey bar indicates the transpiration rate of intact leaves. Species inducing an increase in leaf transpiration (to the left of grey bar) cause the leaf surface to cool down, while species decreasing leaf transpiration rate (to the right of the grey bar) lead to a warming of the surface. Colors indicate feeding guild: phloem feeders in green, leaf miner in blue, and tissue piercers in red.

In the intertidal, the ochre sea star shows particular adaptations to cope with extreme body temperatures: (i) the ability to increase thermal inertia by accumulating sea water into the body cavity (Pincebourde et al. 2009), and (ii) the capacity to derive heat from the central disc to one or several arms that will be sacrificed via autotomy if they get hurt irremediably (Pincebourde et al. 2013). Both strategies allow survival under quite challenging body temperatures. These extreme aerial body temperatures very rarely occur at low tide at least at our study site in the North of California (Pincebourde et al. 2008; Monaco et al. 2016). This study site might not be the most thermally challenging location along the West coast of the US (Helmuth et al. 2002), and the populations are not very well structured genetically suggesting a strong mixing at the pelagic larval stage (Harley et al. 2006). The sea star rarely

approaches its upper lethal temperature limit even if it stays within the mussel bed at low tide all year long. Nevertheless, this set of studies indicates that even rare thermal events may drive or at least select for the conservation of complex thermal adaptations in a predator.

*Conclusion* - The microclimatic temperature generates selective pressures that lead to very subtle thermal adaptations in ectotherms. Species living in the same microhabitat may have different thermal adaptations because of cryptic changes in their microclimate at very fine scale. Another important question is how frequent extreme temperatures should be to significantly drive thermal adaptations? Our set of studies provides first answers. For herbivores, we estimated that the 99th percentile of the air temperature best explains the thermal limit pattern in the community on apple. For the sea star, we estimated that the thermal limit relates best to the absolute maximal hourly air temperature of the year. Therefore, it seems that rare temperatures occurring at a fine temporal resolution are driving thermal adaptations in ectotherms.

*e) Microclimates modulate species interactions*

The microclimate mosaic can modulate species interactions via two mechanisms. The microclimatic mosaic can be exploited differently by the interacting species to the point that the species find different thermal niche allowing them to decrease species interaction strength. Alternatively, species interaction strength can increase when the species are forced to converge towards the same thermal niche. The second mechanism corresponds to a more direct effect of microclimatic conditions on the ecophysiological rates that link the interacting species, including feeding/predation rate or locomotion when escaping/attacking.

My research on insect-plant interactions generates predictions on the issues of competitive interactions among arthropod herbivores at the surface of leaves. As shown above, herbivore species have a different effect on leaf transpiration rate and hence on leaf temperature when feeding on leaf tissues (Pincebourde & Casas 2019). The thermal limit of these arthropods is specifically adapted to their microclimatic conditions (see above). The subtle effects of each herbivore on gas exchange in its host plant have implications at the community scale (Pincebourde & Casas 2019). With the exception of the two aphid species, these herbivores are only

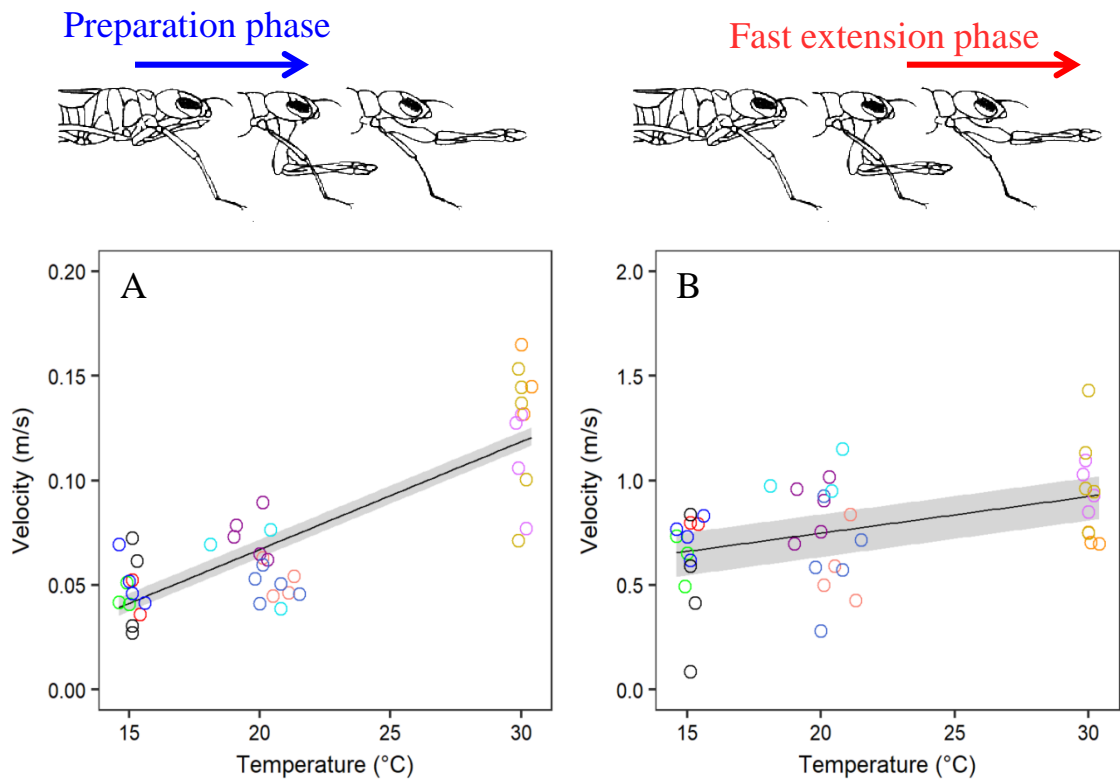
rarely found together on the same apple tree, although they can coexist in the same orchard. Strong competitive interactions between these herbivores probably prevent them from coexisting on the same leaves at the same time in the growing season, although competition by exclusion alone may be too simplistic to explain herbivore assemblages (Kaplan & Denno 2007). The two aphid species can be observed on the same apple tree, but on different leaves (Evenhuis 1964; Simon et al. 2006): The rosy apple aphid mostly develops on leaves in the shade, whereas the green apple aphid is found on apical leaves exposed to full sun (Whitaker et al. 2006). This suggests niche partitioning consistent with their thermal tolerance limits, but this process has never been studied in detail in these species. The application of thermal adaptation theory to our findings would result in a prediction that the two-spotted spider mite, which has the highest thermal limit, should exclude the other herbivores under extreme environmental conditions if all are present on the same plant at the same time. However, there are currently no data available to test this prediction. Communities of arthropods in the phyllosphere could be used as a system model to link community processes and microclimate mosaics within especially complex microhabitats, particularly given that plant biochemistry can also modulate herbivore interactions (Schuman & Baldwin 2016).

In the intertidal ecosystem, we looked at the direct effect of temperature on a predator feeding rate (Pincebourde et al. 2008; Pincebourde et al. 2012). The ochre sea star feeds on mussels in the rocky intertidal. Feeding activity occurs only when the sea star is submerged, at high tide. Aerial body temperature influences the predation rate of the sea star by inducing heat stress, thereby inducing changes in the overall metabolism and in the energy allocation to foraging (Fly, Monaco, Pincebourde & Tullis 2012). Under controlled laboratory conditions, we separately examined the roles of short-term (acute) and long-term (chronic) exposures to high aerial body temperatures in driving patterns of feeding and growth. Although sea stars never approached their upper thermal limit (35°C), laboratory trials demonstrated that chronic exposure to realistic peaks of aerial body temperatures (~28°C) negatively affected both feeding and growth rates, whereas acute exposure had positive consequences on feeding rates but no effects on growth. Variations in aerial body temperature, and more specifically the frequency of exposure to high body temperatures, can influence interaction strength in this important predator–prey system. This study (Pincebourde et al. 2008) became rapidly a 'classics' among the

community of intertidal researchers because for the first time we showed that aerial body temperature induces complex responses that are frequency-dependent in this keystone species. Further, we discovered that the predator feeding rate is related to the interaction between water temperature and aerial body temperature in a complex fashion involving temporal patterns of the two variables ([Pincebourde et al. 2012](#); but see below).

In the freshwater ecosystem, we focused on the impact of water temperature on the biomechanics of a prey-predator interaction. In the aquatic environment, temperature can directly influence the attack behavior by driving the underlying physiological mechanisms but also indirectly by inducing changes in the viscosity of the water. Dragonfly larvae are an interesting model to test for the relative importance of these two effects of water temperature because the larva catches its prey using its labial mask, a prehensile structure containing hooks that is 'launched' towards the prey at a high speed. Based on the speed-accuracy trade-off concept (Chittka et al. 2003), we hypothesized that the increase in predator attack velocity by increasing temperature reduces the accuracy of the attack, leading to a lower probability of capture ([Quenta Herrera, Casas, Dangles & Pincebourde 2018](#)). We tested this hypothesis on the dragonfly larvae *Anax imperator* and the zooplankton prey *Daphnia magna*. The prey-predator encounters were video-recorded at high speed, and at three different temperatures. Overall, we found that (1) temperature had a strong effect on predator's attack velocities, (2) prey did not have the opportunity to move and/or escape due to the high velocity of the predator during the attack (around 25 cm per second!), and (3) neither velocity nor temperature had significant effects on the capture success. By contrast, the capture success mainly depended on the accuracy of the predator in capturing the prey. These results did not support the speed-accuracy trade-off hypothesis. Interestingly, however, the extension of the labial mask shows two phases: it is first slowly adjusted toward the prey, and secondly it is launched at very high speed toward the prey. Contrary to our expectations, the time taken for the first phase of preparation is highly temperature-dependent (faster at high temperature) while the second phase barely depends on temperature (Figure III.17). The adjustment of the mask may integrate sensorial systems that are linked to the metabolism of the insect while the high-speed launch of the mask seems to involve a hydraulic-pumping strategy that could be independent to the general metabolism. We think that the temperature-induced changes in water

viscosity should influence mostly the second phase of the attack. This effect remains to be tested in the lab.



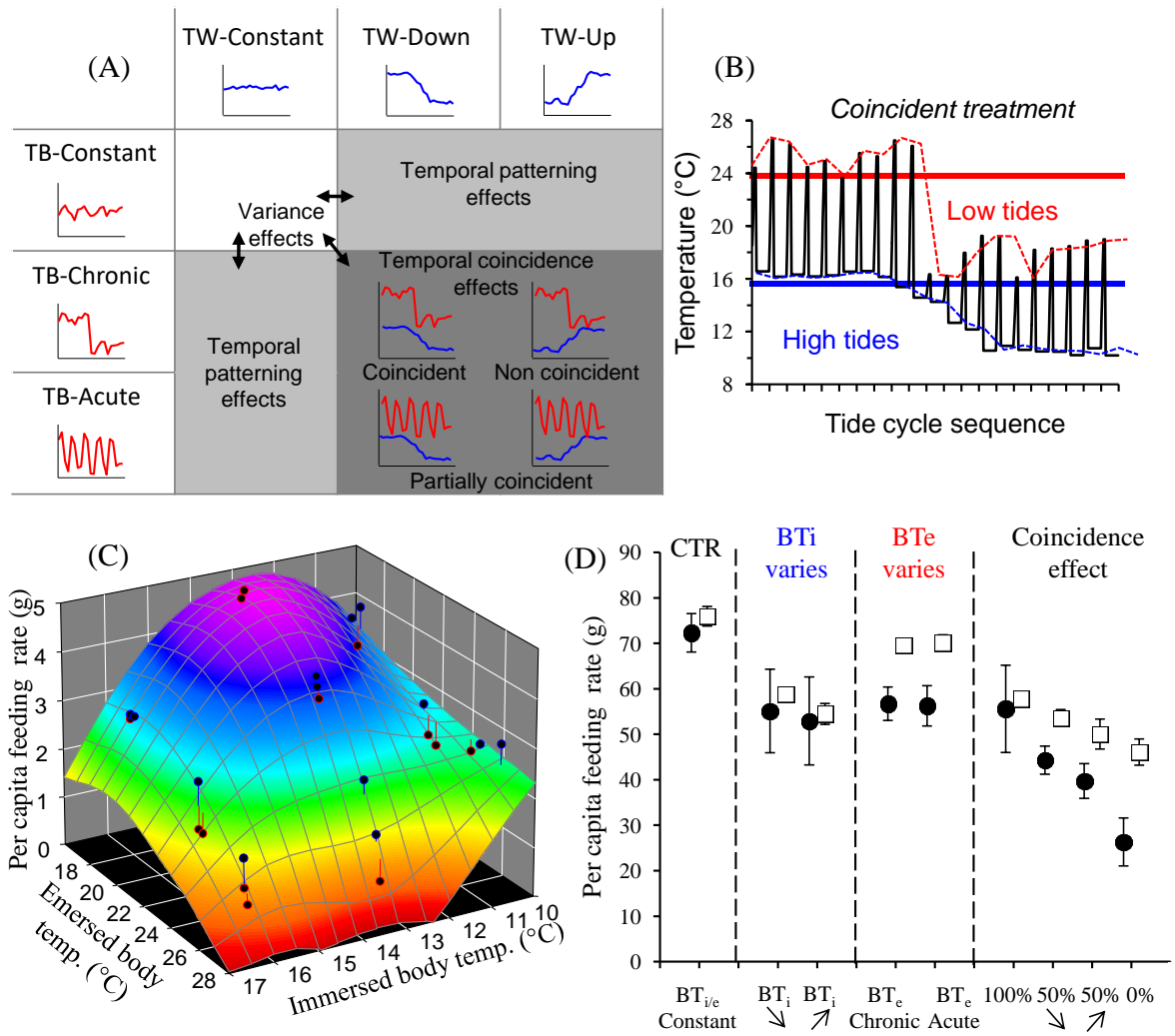
**Figure III.17.** The effect of water temperature on the velocity of the labial mask of the dragonfly larva during the two phases of mask extension: (A) during the preparation and adjustment of the mask and (B) during the fast extension of the mask. Different colors indicate the 11 different individuals. The gray shade gives the 95% interval of the linear regression. Note the 10-fold scale difference between the two velocities.

**Conclusion** - Arguing that the influence of temperature on biotic interactions is poorly understood is obviously not true anymore (this argument appears quite often in the introduction of contemporary publications). The literature on effects of temperature on feeding rates abounds. However, the (ecophysiological and biomechanical) mechanisms involved are not always clear and this should be the focus of next generation of studies on the temperature effects on biotic interactions.

*f) Apprehending the complexity of microclimates*

The sections above deal mostly with the temperature of the microclimate or the organism's body. Temperature is a major driver of physiological rates (Somero 1995). But the analysis of microclimates is far more complex than looking at the sole effect of absolute temperature on ectotherms (Benedetti-Cecchi 2003). The first level of complexity comes from time (Benedetti-Cecchi et al. 2006). Temperature is fluctuating in time but the patterns of variation may differ depending on the temporal scale and the particular environmental context. Two of my studies illustrate this point.

The ochre sea star experiences water temperature at high tide. At low tide, the body temperature of the sea star is driven by aerial environment (mostly radiation level, wind, air temperature). Therefore, while the two variables are temperature, they can be analyzed separately, especially given that in the field there is no or little correlation between them. This means that during a single tide cycle, any aerial body temperature can be obtained at any water temperature level (Pincebourde et al. 2012). Stressful aerial body temperature can be reached whenever water temperature is low or high. Therefore, with Prof. Brian Helmuth and Prof. Eric Sanford, we designed an experiment in the lab to simulate the different scenarios with varying levels of temporal coincidence between stressful temperatures while underwater versus aerial exposure (Figure III.18). The treatments were designed to separate the effect of mean temperature, variance of the temperature, and the temporal pattern of the fluctuation (an infinite number of patterns exists with same mean and variance). We measured the response of predation rate to these scenarios. We expected to see a lower predation rate when thermal stress occurs synchronal during the same tide cycles underwater and in the air because of stress accumulation. Surprisingly, we obtained the reverse. Predation rate was higher when the two stressors coincided temporally compared to when the two stressors occurred sequentially during different tide cycles (Figure III.18). Scenarios with partial temporal coincidence gave intermediate results (Figure III.18). Therefore, investigating mean and variance effects of environmental temperature on organisms is not enough. Temporal issues of the fluctuation patterns are at least as important.



**Figure III.18.** Quantifying the effect of temporal coincidence between two stressors on the predation rate of the ochre sea star. (A) The two experimental variables are the body temperature at low tide (emmersed temperature  $BTe$ ) and when underwater at high tide (immersed temperature  $BTi$ ). This schematic indicates which comparisons of thermal treatments allow assessment of the influence of variance around the mean (double-headed arrows: comparison of constant vs. one factor varying treatments), temporal patterning (light grey boxes: comparison among one factor-varying treatments) and level of temporal coincidence (dark grey box: comparison among all two factors-varying treatments) on feeding rate. (B) An illustration of how the treatments were designed. Each sequence is a tide cycle (about 18 hours) with aerial body temperature going high at low tide and underwater temperature is always cooler than in the air. Blue and red bands indicate the thermal stress thresholds for  $BTi$  (at  $15.5^{\circ}C$ ) and  $BTe$  (at  $24^{\circ}C$ ), respectively. (C) Per capita feeding rate of *Pisaster ochraceus* (expressed per tide cycle) as function of emersed body temperature ( $BTe$ ) and immersed body temperature ( $BTi$ ) under constant conditions. (D) Per capita feeding rate of *P.* (total for the 20 days) as function of thermal treatments shown in (A). Black points represent experimental means ( $\pm$  SD) and white squares indicate the predictions (mean  $\pm$  sd) of the interpolated model shown in (C).



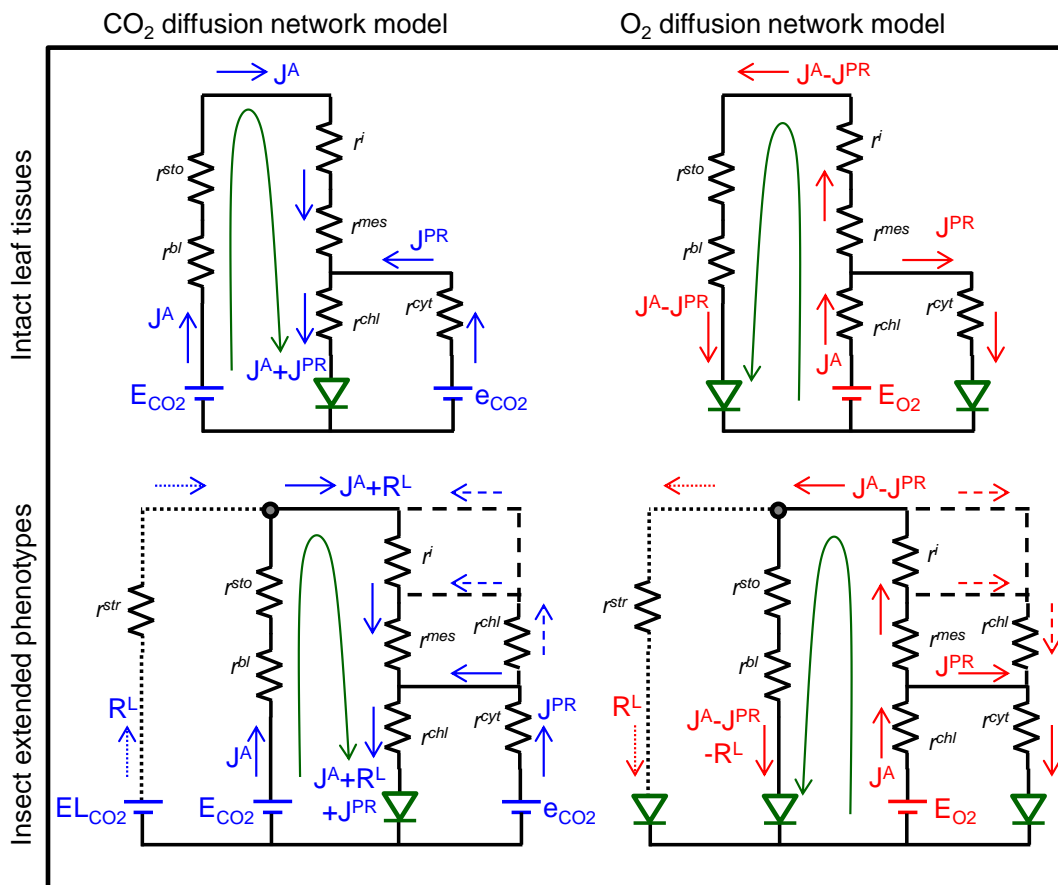
Indeed, organisms living in fluctuating environment spend little time at the mean temperature (most of the time they are above and below the mean). With a working group at an annual meeting of the Society for Integrative and Comparative Biology in 2016, we expanded on this role of temporal fluctuations in temperature on biological processes by dissecting and partitioning the amount of temporal variance at various temporal scales from minute, daily or weekly to monthly and yearly scales (**Dillon, Woods, Wang, Fey, Vasseur, Telemeco, Marshall & Pincebourde 2016**). We developed a framework both for analyzing temporal patterns of temperature variation and for incorporating those patterns into predictions about organismal biology. In particular, we proposed the use of the Fourier transform to decompose temperature time series into their component sinusoids, thus allowing transformations between the time and frequency domains. This approach provides (1) standardized ways of visualizing the contributions that different frequencies make to total temporal variation; (2) the ability to assess how patterns of temperature variation have changed over the past half century and may change into the future; and (3) clear approaches to manipulating temporal time series to ask *what if* questions about the potential effects of future climates. We then demonstrated the utility of the Fourier framework by exploring how power added to different frequencies alters the overall incidence of long-term waves of high and low temperatures, and find that power added to the lowest frequencies greatly increases the probability of long-term heat and cold waves. Analyses of microclimatic temporal series using Fourier transforms remain to be done however (but see Faye et al. 2014).

Microenvironments are often (if not always) multifactorial. In addition to temperature, the nutritional resource is obviously an extremely important environmental factor determining the performance of ectotherms (Simpson et al. 2010). The level of the resource can fluctuate in time, both qualitatively and quantitatively. In a review that I led with international collaborators (**Pincebourde et al. 2017**), we highlighted the complexity of the interactions between several factors in insect-plant relationships. The chemical defenses of the plant, the nutritional quality of the plant tissues and the plant gas exchange directly influence the growth rate of the herbivore insect. Yet, little is known on the potential interactive effects between these factors. In another collaboration, I participated to the development of a theoretical and conceptual framework to integrate the variance effects of each

environmental factor, and the covariance effect of these interacting factors, on the performance of an ectotherm. This work was led by Apostolos Koussoroplis (**Koussoroplis, Pincebourde & Wacker 2017**). We applied the scale-transition theory (Chesson et al. 2005) to predict the physiological performance under fluctuating and multifactorial environments depending on the level of covariance between the multiple factors. This approach allows one to quantify the effects of covariance on performance and the role of synergy, antagonism and additivity. This approach can be used to detect mechanisms such as acclimation and physiological stress when they are at play. We showed that the statistical covariance of co-limiting factors, which has not been considered before, can be a strong driver of physiological performance in various ecological contexts. Our framework can provide powerful insights on how the global change-induced shifts in multiple environmental factors affect the physiological performance of organisms.

From these conceptual developments, I searched for environmental variables that are tightly linked to temperature and biological processes so we can experiment on the role of limiting factors and their level of covariance on the performance of ectotherms. Gas composition (e.g., O<sub>2</sub> and CO<sub>2</sub>) is another important aspect for the physiology of ectotherms (Verberk et al. 2011; Harrison et al. 2018), in particular for organisms living within small galleries or nests such as endophagous insects (leaf miners, gall-inducers, stem borers etc.). Gas diffusion may be slower within such structures than for organisms exposed to open air. We reviewed what is known on the gas composition within the structures developed by endophagous insects (**Pincebourde and Casas 2016**). Amazingly, very little is known on the degree to which miners, gallers and borers can experience hypoxia and/or hypercarbia by living within plant tissues. Therefore, we developed a theoretical model of gas diffusion within these structures to make predictions on the probability to reach hypoxic/hypercarbic conditions. We developed a conceptual framework to show how the structure of galls and mines sets the resistance networks for CO<sub>2</sub> and O<sub>2</sub> diffusion within them, determining thereby the risk for hypercarbia and hypoxia, respectively. A similar approach has been used for decades to study gas limitation in the context of plant photosynthesis. In plant ecophysiology, the various gas fluxes, resistances, and rates of photosynthesis and (photo) respiration can be integrated into a single analytical framework using an electrical circuit analogy (Nobel, 1999). This approach was developed mostly to describe CO<sub>2</sub> fluxes through a leaf. We extended

the method to describe the patterns of CO<sub>2</sub> and O<sub>2</sub> diffusion to the insect across its microhabitat (Figure III.19). Briefly, using this model, we ranked the various endophagous herbivore lifestyles in terms of increasing risk of exposure to hypoxia and hypercarbia: upper and lower-surface mines, aquatic mines, bark mines, galls (small then large), tunnels (borers), and cambium mines. This ranking is expected to vary across insect species, but we proposed it as a general pattern. We are currently starting to test these predictions experimentally on galls of different sizes (see *Part IV: Research perspectives*).



**Figure III.19.** Conceptual model of the resistance pathways along diffusion of CO<sub>2</sub> (blue, left panels) and O<sub>2</sub> (red, right panels) in intact plant tissues (upper panels) and in tissues attacked by an endophagous insect larva (lower panels). CO<sub>2</sub> sources are ambient air (battery of electromotive force,  $E_{CO_2}$ ), (photo) respiration sites ( $e_{CO_2}$ ) and larval respiration ( $EL_{CO_2}$ ). Chloroplasts produce O<sub>2</sub> during photosynthesis. The currents of the circuit (arrows) correspond to amounts of gas that diffuse through the system ( $J^A$  for the net assimilation rate,  $J^{PR}$  for the photorespiration rate and  $R^L$  for the insect respiration rate). Green arrows indicate the main loop of the electrical circuit that defines gas diffusion through leaf tissues. Alternative loops are present when an insect larva is positioned in the intercellular space (dotted-line pathways) or when new respiring plant tissues are developed (dashed-line pathways). Grey dots represent location at which the CO<sub>2</sub> emitted by a larva joins the main

pathway. Legends of the resistances: boundary layer ( $r^{bl}$ ), stomata and/or epidermis ( $r^{sto}$ ), intercellular air space ( $r^i$ ), mesophyll tissues ( $r^{mes}$ ), cytoplasm media ( $r^{cyt}$ ), chloroplast membranes ( $r^{chl}$ ) and the habitat of the larva ( $r^{str}$ ) which can be reduced to air space with a resistance similar to  $r^i$  for instance. The term  $r^{str}$  is general and can represent any type of modification. Adapted and modified from Nobel (1999).

**Conclusion** - Much remains to be done to integrate the full complexity of fine-scale microclimates into a single framework of species thermal traits. Temperature-independent traits can cascade to other traits that have an impact on the heat budget of ectotherms. These indirect links could confuse results in studies looking at the adaptive value of thermal trait variations. These multiple interactions between fluctuating factors generate variance and covariance effects that we are only starting to comprehend.

#### 4. The vulnerability of ectotherms to climate change

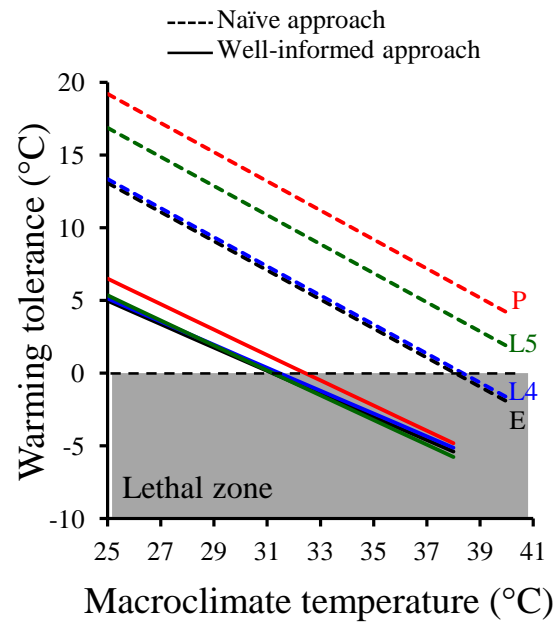
The work I detail above has strong implications on the assessment of vulnerability of ectotherms to climate change. Below, I illustrate how microclimatic ecology changes the way we think about the potential ecological impacts of climate change based on two chapters.

##### a) *The vulnerability of herbivores to heat waves*

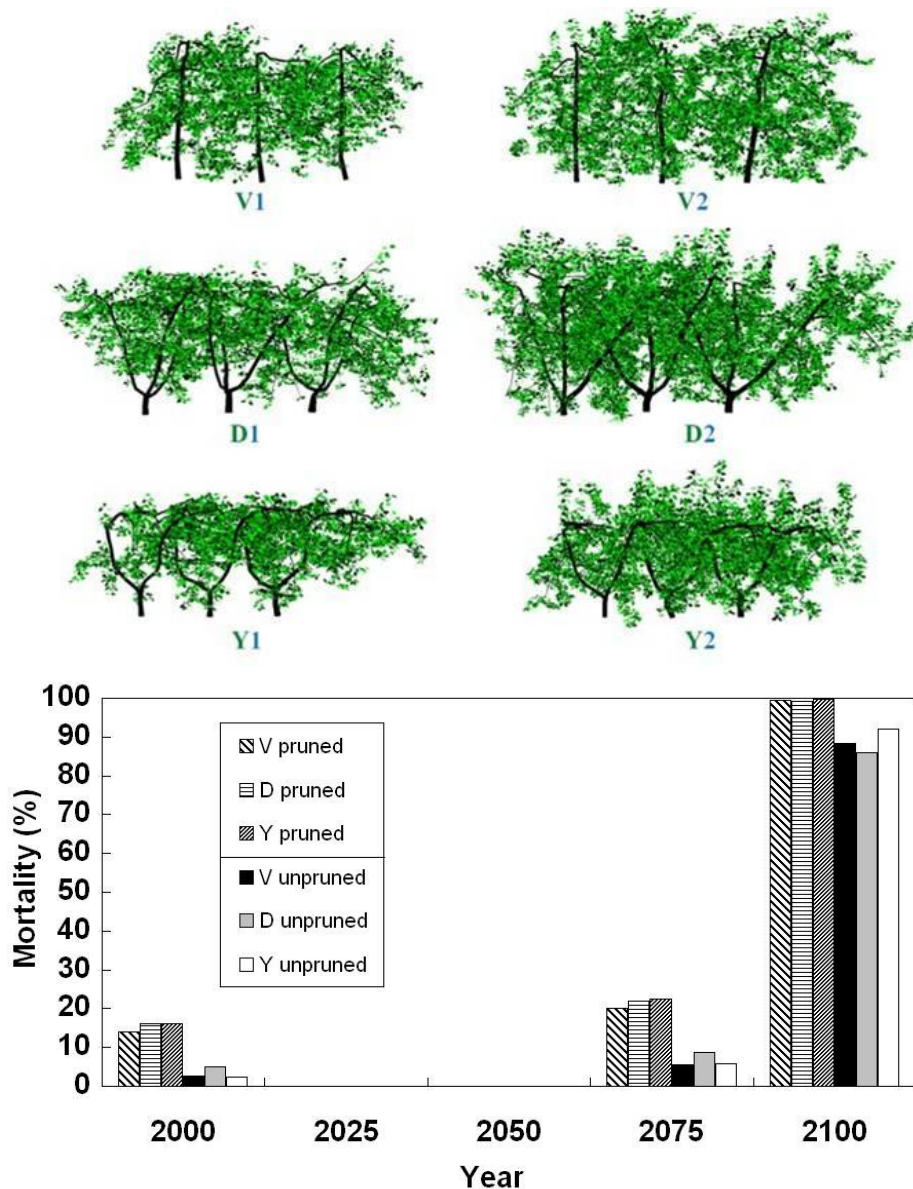
To what extent knowledge on thermal limits and/or microclimates help us estimating the vulnerability of ectotherms to climate change? The apple leaf miner case above (see Figure III.15) provides an excellent example to explain why two different typical approaches are endlessly fighting against each other. If we refer only to the thermal limits to rank the various developmental stages of the leaf miner from the less to the most vulnerable to climate warming, one concludes that the egg stage is more at risk than nymphs because they are much less tolerant to high temperatures (Figure III.15, right panel). By contrast, based only on the microclimatic patterns, one concludes that the nymph stage is more at risk of overheating than eggs during warming because they are already living in a warmer microenvironment (Figure III.15, left panel). Therefore, we end up with two opposing predictions. These two

metrics have to be integrated with each other when quantifying the degree to which ectotherms are vulnerable during warming.

The vulnerability of ectotherms to climate change can be estimated using the thermal safety margin concept (Garcia et al. 2019). This approach compares thermal traits of species (e.g., the CT<sub>max</sub>) with environmental temperature metrics. The species is 'safe' as long as thermal trait remains above the environmental temperature, but it becomes vulnerable once a threshold is reached (Sunday et al. 2014). The concept of 'warming tolerance' is a simple way to quantify this thermal safety margin (Deutsch et al. 2008; Scheffers et al. 2013). Warming tolerance is the difference between the thermal limit of a species and environmental temperature. The species is safe when warming tolerance is positive and becomes vulnerable when it is negative. The species has no safety margin when warming tolerance equals zero. The studies that used the warming tolerance concept mostly used the atmospheric temperature in the calculation - an approach said to be naïve because it neglects the importance of microclimatic deviations relative to ambient air (Scheffers et al. 2013). By contrast, we encourage ecologists to employ the microclimatic temperature instead of air temperature — we call this a well-informed approach (**Pincebourde & Casas 2015**). We calculated the warming tolerance for each stage of the apple leaf miner using the two approaches, naïve and well-informed (Figure III.20). We showed that the naïve approach overestimates by  $>7^{\circ}\text{C}$  the warming tolerance. Importantly, while the naïve approach predicts different trajectories for warming tolerance across the different developmental stages, the well-informed method indicates clearly that all stage are equally vulnerable to warming despite the differences in thermal limits (Figure III.20). This example indicates that integrating microclimatic patterns into vulnerability assessment frameworks for climate change impacts is mandatory. Indeed, the microclimate of a mine explains the trend in mortality in simulations under climate scenarios by 2100 among leaf mines in apple trees with different canopy architecture (**Saudreau, Pincebourde, Dassot, Adam, Loxdale & Biron 2013**). Unpruned trees will provide denser foliage and will protect a small portion of the population from getting high radiation doses that will overheat to death most of the individuals (Figure III.21).



**Figure III.20.** Habitat-specific, well-informed warming tolerance (upper lethal temperature, ULT, minus microclimate temperature; solid lines) and naïve warming tolerance (ULT minus macroclimate temperature; dashed lines) as function of macroclimate temperature across ontogeny: eggs (E; black lines), L4 (blue lines), L5 (green lines), and nymphs (P; red lines). Positive and negative values indicate the ranges of tolerable and critical (gray portion) temperatures, respectively. The microclimatic temperature was computed using the biophysical model of mine temperature. The temperature within the mine was simulated at high radiation load and for different air temperature values (called macroclimate temperature here).

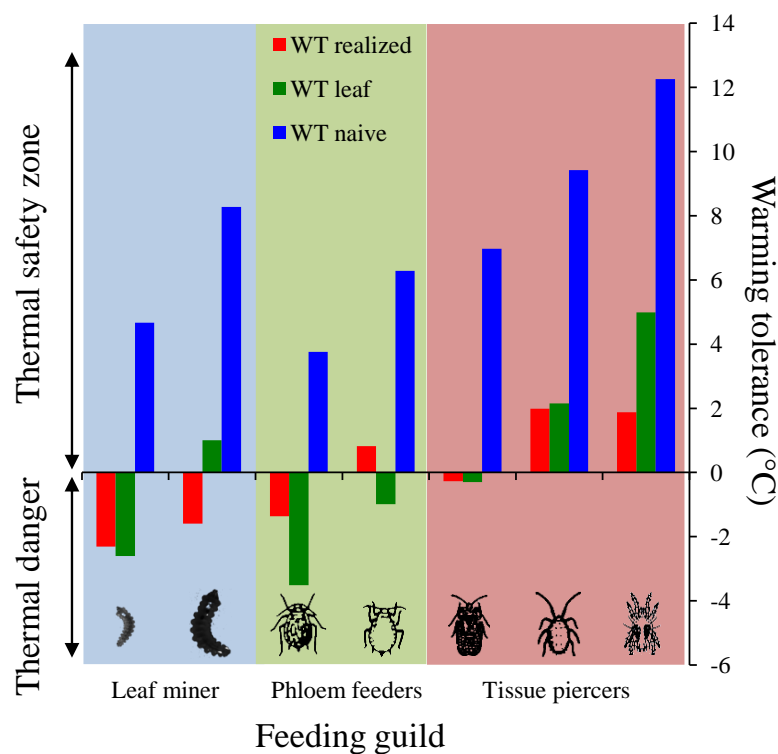


**Figure III.21.** The different architecture of apple trees have an effect on mortality of *P. blancardella* at the 5th larval instar for six 3D apple tree mock-ups of real orchards during July periods in the 21st century at the city of Avignon (France). No heat-related mortality was predicted during the other months. This result was obtained by combining a physical model of radiation transfer across tree canopies and the biophysical model of heat budget of a leaf mine.

We generalized the vulnerability approach developed above on the apple leaf miner to arthropods living in the leaf microclimate (Pincebourde & Casas 2019). We quantified the warming tolerance of these herbivores that differ in their thermal limit as well as in their microclimatic temperature (see above). Warming tolerance was calculated during the conditions of a heat wave that we had in spring 2012. We



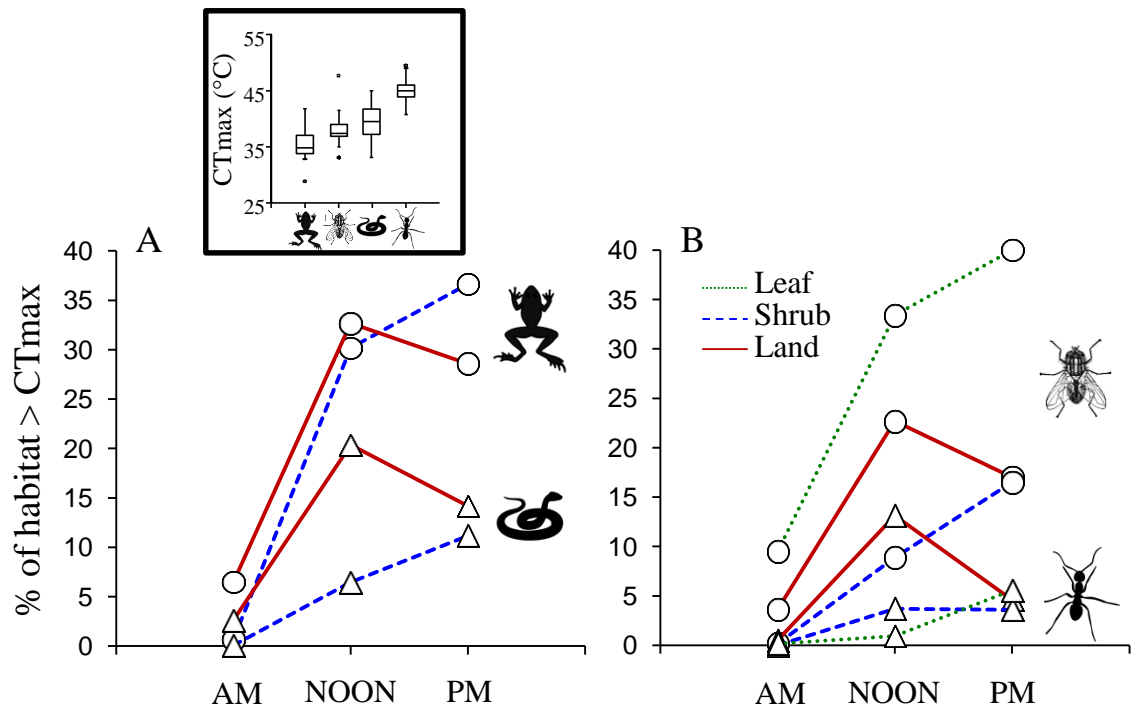
found that the naïve approach (using air temperature instead of microclimate) overestimates warming tolerance by up to 12°C (Figure III.22). Using the temperature of intact leaves ameliorates considerably the predictions, but it over-estimates or under-estimates the warming tolerance for some of the species because it ignores the effects of these herbivore on the leaf transpiration rate. By contrast, the well-informed approach (realized warming tolerance based on the microclimate temperature when the arthropod feeds on the leaf) demonstrates that the thermal safety margin for all arthropods is relatively small (more or less 2°C). Globally, leaf miners and phloem feeders may be slightly more at risk than tissue piercers under heat wave events (Figure III.22). This study is important as it shows that fine-scales processes already put temperate arthropods near their own thresholds, contrary to macroecological studies showing the reverse because they ignore these fine-scale effects (e.g., Deutsch et al. 2008; Pinsky et al. 2019).



**Figure III.22.** Thermal safety margin as function of the tightness of coupling between the herbivore and the leaf. The warming tolerance (WT) of each arthropod species was calculated using the surrounding air temperature (blue bars, erroneous naïve approach), the temperature of intact leaves (green bars, a mostly erroneous approach) and the attacked leaf temperature (red bars, the best estimate). Warming tolerance quantifies the amplitude of warming that a species can tolerate before it dies under a given set of conditions. Herbivorous species are arranged according to their feeding mode (background colors: pale blue: leaf-mining, pale green: phloem-feeders, pale red: tissue-piercers).

*b) The influence of thermal heterogeneity on vulnerability*

Ectotherms may be more vulnerable to heat waves than expected once one incorporates microclimatic conditions into the framework (see above). However, the thermal heterogeneity at various spatial scales may rescue these ectotherms, especially when they use behavioral thermoregulation (Sunday et al. 2014). In a review with international collaborators, we highlight that almost nothing is known on how climate change will modify the thermal mosaics for ectotherms at land versus local versus very fine spatial scales (**Pincebourde, Murdock, Vickers & Sears 2016**). Currently, this is a missing link in global change biology. In our empirical study done in an extreme thermal habitat, the top of a granitic inselberg in a tropical forest (French Guiana), we provided the very first analysis of this kind. The spatial variance of surface temperatures is high in this environment at all spatial scales (see Figure III.8). We compared the surface temperature distributions taken with an infrared camera with the mean CT<sub>max</sub> of various taxa of tropical ectotherms that we retrieved from the literature (**Pincebourde & Suppo 2016**). We found overall that less than half of the habitat showed surface temperatures that were above the thermal limits of ectotherms (Figure III.23). Interestingly, the portion of the habitat that is dangerous for ectotherms varies between the spatial scales (landscape versus shrub versus single leaf scale). For example, insects would have better chances to survive when moving at the scale of the single shrub compared to moving across the landscape or across a single leaf surface (Figure III.23). The vulnerability of ectotherms also varies across the day, providing a complex spatio-temporal mosaic of vulnerability to environmental changes.



**Figure III.23.** Estimated vulnerability of ectotherms, based on the portion of temperature distributions that fall above the mean  $CT_{max}$  of organisms, for morning, noon and afternoon periods. (A) For amphibians (circles) and reptiles (triangles) at shrub (blue dashed lines) and landscape (red full lines) scales. (B) For insects (circles) and ants (triangles) on sunny leaves (among sunny leaf scale; green dotted lines), at shrub (blue dashed lines) and landscape (red full lines) scales. The inset shows the maximal critical temperature threshold ( $CT_{max}$ ; retrieved from the literature) of amphibians, insects, reptiles and ants (box plots).

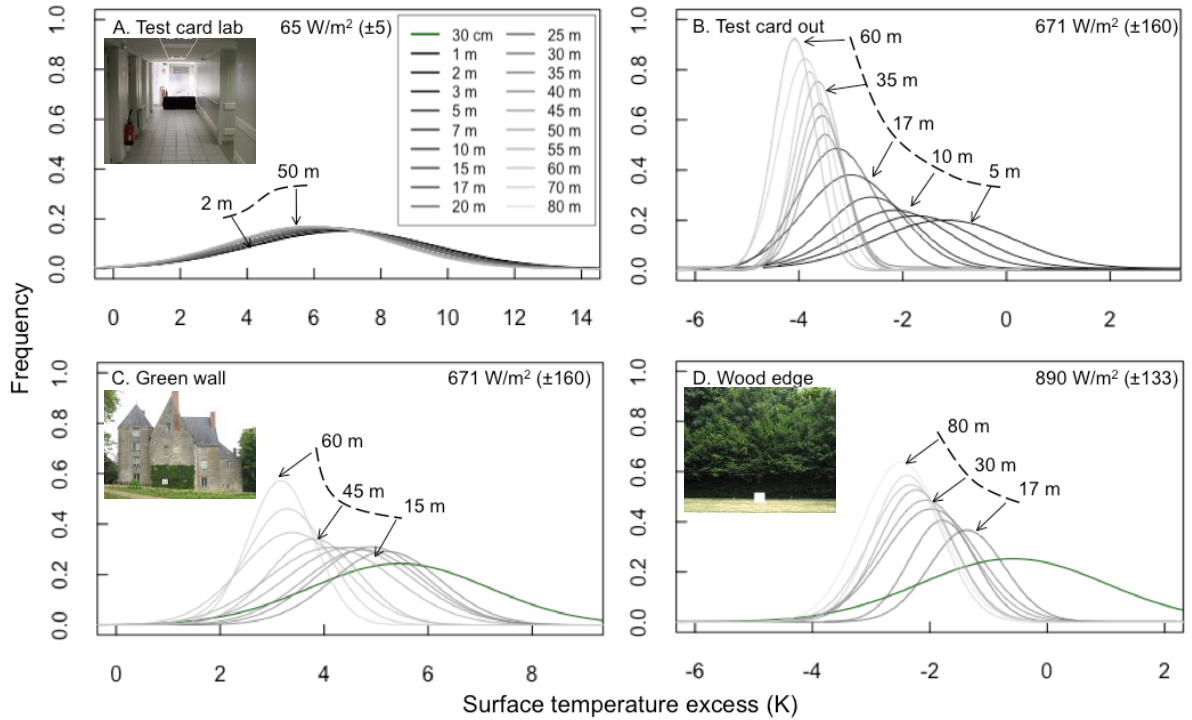
## 5. Methodologies: measuring and modeling biophysical processes

The research I detail above necessarily implies to adjust or improve some methodologies. Here, I focus on two aspects that are important for my research: thermal imaging and biophysical modeling.

### a) Thermal imaging: application to insect-plant interactions

Thermal imaging (or thermography) is an important methodology for my research. I use thermal imaging to quantify the level of *spatial* variance of surface temperature. This tool combines very well with temperature loggers (e.g., hobo) which are used to measure the *temporal* variance of temperature. In particular, we

used thermal imaging to characterize the distribution of surface temperature over single leaves (**Saudreau, Ezanic, Adam, Caillon, Walser & Pincebourde 2017**). We were also the first team to record simultaneously leaf surface temperature and the movement of arthropods at the leaf surface (**Caillon, Suppo, Casas, Woods & Pincebourde 2014**). Finally, we also used thermal imaging to compare the level of thermal heterogeneity available for ectotherms at different spatial scales (**Pincebourde & Suppo 2016**). Across these studies, one pertinent question came naturally to us: what does the infrared camera do when the distance to the object increases? An infrared camera has a fixed array of infrared sensors and each sensor generates a single pixel on the thermal image (e.g. 320 x 240 sensors generate 76,800 pixels). Thus, when the camera is close to the leaf surface, a single pixels covers much less than 1mm<sup>2</sup> of the surface (high spatial resolution) while when the camera is positioned far from the leaf, a single pixel includes the whole leaf plus some background (low spatial resolution). In this case, does the corresponding sensor measure the mean leaf surface temperature for instance? Or is there a bias? I collaborated with a PhD Student of Olivier Dangles to design careful experiments to quantify the effect of distance between the camera and the object on temperature readings (**Faye, Dangles & Pincebourde 2016**). Infrared images of various surfaces were taken along distance transects. We found that increasing distance caused both an under-estimation of the extreme temperature and a spatial homogenization of temperatures. We also found that shooting distance significantly modified the surface temperature distribution in the outdoor environments. Leaf temperature distributions, taken at a distance of 0.3 m from the surface (green curves in Figure III.24) showed larger temperature range and lower density maximum than the entire vegetation background in the green wall and wood edge environments (Figure III.24). All statistical metrics were altered by the distance. For example, the mean surface temperature decreased by 3.4 °C during only the first 20m of the distance transect – indeed the under-estimation was non-linearly linked with distance.



**Figure III.24.** Frequency distribution of the surface temperature excess (K) obtained from thermal infrared images of the mobile camera at various distances for the 1 m<sup>2</sup> thermal test card in the laboratory and in the green wall environments (A and B, respectively), of the whole surface of the green wall (C) and of the whole surface of the wood edge (D) under clear sky conditions. Green curves in C and D represent the leaf surface temperature distributions from TIR images taken at 0.3 m from individual leaves of the green-wall and the wood-edge respectively.

**Conclusion:** Thermal imaging is now largely used for various topics in biology. Cameras are becoming more powerful (e.g., higher resolution) and they are now affordable. Nevertheless, researchers have to use these cameras carefully as several pitfalls were identified. The effect of distance to the object that we quantified is one of these problems that need to be considered especially in studies comparing thermal images taken at different distances.

*b) Biophysical modeling: the heat budget of ectotherms*

Biophysical modeling is another crucial tool for my research. This mechanistic approach of computing the heat budget of an organism allowed me to better understand the flux of energy in and out of an ectotherm or a plant. My research contributed to the development of these mechanistic models. We were the first to integrate the heat budget of the plant and its herbivore into a single model (Pincebourde & Casas 2006a). The heat budget of the insect (the leaf miner) cannot

be understood without the integration of the leaf heat budget. Later, we implemented this same model to integrate the dynamics of the leaf miner thermal environment across its ontogeny (**Pincebourde & Casas 2015**). Recently, we applied this same biophysical approach to several herbivore species feeding externally at the leaf surface (**Pincebourde & Casas 2019**). Therefore, our studies (and others especially by Michael Kearney and Brian Helmuth) demonstrate the plus-value of using these mechanistic models to predict microclimatic temperatures and to understand which traits can influence the heat budget of ectotherms. Yet, I find amazing that this biophysical approach remains only marginally used by ecologists. The use of this tool is rising significantly since only very recently. Probably, the mathematical and physical concepts included in this tool were first repulsive to most ecologists. The recent developments in R are making the use of these biophysical models more accessible (e.g. NicheMap R; Kearney et al. 2014; *See Part II: overview of the field*).

## 6. A natural history prospect of microclimates

My motivation for academic research finds its roots in my love for nature. I literally devoured the famous books *Souvenirs Entomologiques* of Jean Henri Fabre (1879), a French entomologist who influenced the field at the same time than Darwin (they communicated with each other). I was really marked by the chapters on the *Cerceris* and the *Sphex* which were written while JH Fabre was working in the beautiful region of Aveyron. These stories brought him to have serious doubts about the last theory of Charles Darwin: the theory of natural selection. Hymenopteran of the family Sphecidae capture a prey (spiders, grasshoppers or caterpillars depending on the species), paralyze it, take it into a burrow, lay an egg on it and then the larva feeds on the paralyzed prey to complete its development (Figure III.25). JH Fabre was amazed by the way the Sphecidae attack the prey. In some species, the wasp has to insert its dart at a very precise location into one the ganglion along the nervous chain of the spider or caterpillar, while the prey moves to defend itself. If the prey is loosely paralyzed, then it can start moving again as the egg is on it, thereby destroying the chance of the Sphecidae larva to feed on it. On the other hand, the Sphecidae larva has no chance either if the prey is killed by darting at the wrong



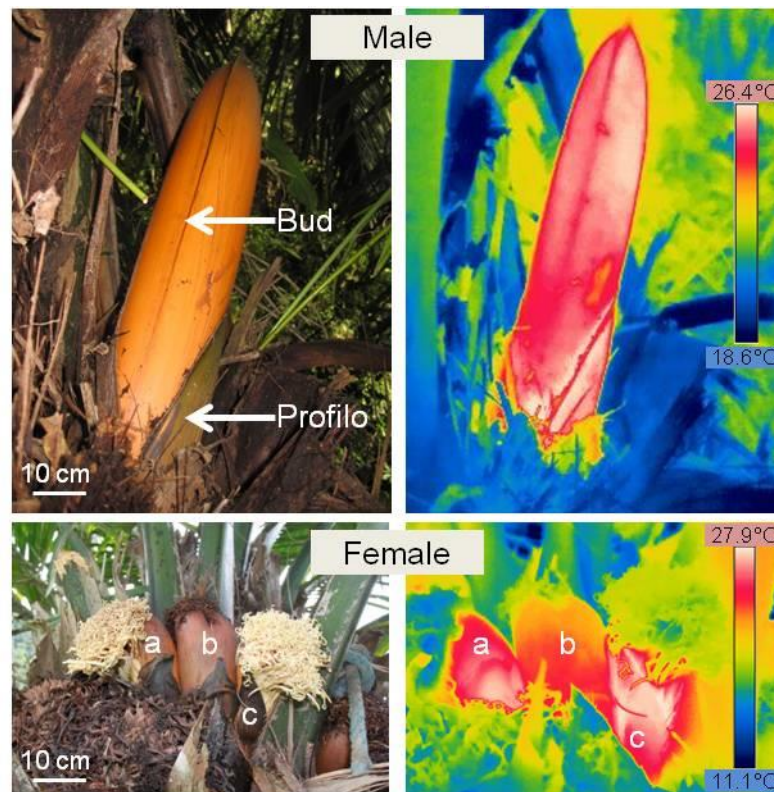
place. JH Fabre asked himself how many failures before a first success. How probable for an individual in the population to suddenly find the right location in the right ganglion to indefinitely paralyze the prey without killing it? How this theory of natural selection can reasonably explain this level of 'luck'? Obviously, JH Fabre neglected the possibility for coevolution between the predator and its host, from a much more simple interaction before the arm race took place and derived towards such a level of sophistication. These lines of JH Fabre really influenced my view of how to integrate natural history into academy research: natural observations first, which generate working hypotheses, then experimentation to test them.



**Figure III.25.** Hymenopteran of the family Sphecidae are amazing creatures. Here the main photograph shows a *Sphex* (taken in SC, USA) which just captured a grasshopper. The grasshopper is not dead (not yet...): it is paralyzed after the female sting into a particular ganglion. Then, the *Sphex* digs a burrow (inset left), and places the grasshopper inside it (inset right). The female will lay a single egg on the paralyzed body. The larva will feed on the grasshopper body while it is alive, starting by eating on the non-vital parts to insure it has 'fresh' meat until end of the development.



In this philosophical context, I always have been particularly attracted by thermogenic plants, which produce heat to attract or reward their pollinator, or to maximize volatile emission. For this reason, when my colleague Dr. Olivier Dangles told me about a palm tree in Ecuador that may be producing heat at some point, I was very excited to study it. At that time, farmers were the only ones to know about heat production by the flowers of the ivory palm (*Phytelephas aequatorialis*). We were the first to describe thermogenesis in this planted palm, endemic of Ecuador, by combining temperature loggers and thermal imaging in the field (**Pincebourde, Montúfar, Páez & Dangles 2016**). We obtained promising observations that the flower, at the bud stage, thermoregulates. Interestingly, female and male flowers produce different thermal patterns (Figure III.26). Indeed, the two flowers of this palm are different. Male flower extends from ~30 cm up to 2 or 3 m in length in a single night and decays rapidly within 30 hours while the female flower remains relatively small (<40 cm) but live more than a week. Thermal patterns reflect the gigantism of these flowers. As of today, the function of heat production in this palm remains unclear. But we don't necessarily have to fly to South America to observe thermogenic plants. Arum species in Europe are known to produce heat and these plants are widespread. The relationship between the microclimate of the heat-producing flower and the thermal biology of the pollinator remains however understudied (see *Part IV: Research perspectives*).



**Figure III.26.** Photographs (left) and thermographic images (right) of a male flower bud (top) and female flowers with the bud integument remaining at the basis of the flower (bottom). Air temperature was 23.4°C for the male bud and 22.5°C for the female inflorescence. Infrared images show the surface temperature. The temperature within the buds was higher than the surface temperature. Three female inflorescences at different phenological stages are shown, from left to right: (a) late stage, (b) senescent and (c) recently opened. Location: Otonga Reserve (Ecuador).

Carnivorous plants are also an interesting model for microclimate ecology. *Sarracenia* plants develop a long tube-shape trap filled with digestive enzymes (pitcher). The unfortunate insects that fall into the trap are slowly digested. Given our studies on the microclimate of leaf mines and tree leaves, we expect these traps to create particular microclimates. I started to study this in collaboration with Arthur Sanguet who owns an incredible collection of *Sarracenia* species and varieties. We measured the temperature inside traps of different coloration as well as digestive rates, to test if the temperature excess inside the traps may increase digestive efficiency of the enzymes. The work is currently processing.

Twenty years ago, I did a sort of internship program in the National Park of Guadeloupe to contribute to the inventory of insect species in the natural reserve. It was the first time I met tropical Spingid species and I was immediately amazed by

their strong flight abilities, their aerodynamic morphology and their strange behavior they have when they land on the white sheet during a night trap. They stand on the sheet by vibrating continuously their wing muscles. All Sphingid species I observed showed this behavior. This behavior is linked to their endothermy (Heinrich 1996). They have to increase the temperature of their thoracic muscles and maintain it to keep the ability to fly immediately. Much later, I realized that we could measure the temperature of their thoracic muscles using an infrared camera during a light trap, by spotting the individuals immediately after they land on the white sheet. Indeed, the endothermic behavior of Sphingids was never measured in the field before (only in lab settings). We applied this methodology on a community of Sphingid species in Ecuador to investigate if the thoracic temperature remains similar among species and between locations differing in altitude. This study was done in collaboration with Dr. Olivier Dangles and one of his Master students. The work is currently processing.

## 7. Applying microclimate ecology to conservation

Microclimate ecology can provide valuable tools and concepts for conservation of biodiversity. I illustrate this integration using dragonflies as a model. Following the publication of the National Plan of Actions for conservation of Odonates in France in 2010, I established a collaboration with a naturalist association (ANEPE Caudalis) to downscale this national plan to the regional scale, for our region Centre-Val-de-Loire (**Baeta, Sansault & Pincebourde 2012**). Each



administrative region in France did this downscaling to better adjust the national problems and to propose actions according to the regional constraints and concerns. Therefore, in this regional plan (PRAO), we set the agenda for a series of actions from ecological knowledge on particular threaten species to the application of concrete conservation plans, such as the restoration of wetlands in managed forests. This agenda ran for 8 years and finished in 2019. The new National Plan is currently being updated for the next 10 years.

The most important action of the PRAO consisted in coordinating the regional sampling efforts to develop a regional database of species presence and absence. The naturalist association did an excellent job of coordination between the different structures that collect information on species presence. We now have a huge database with species presence through time at a high spatial resolution. The analysis of such database will certainly take years, as some analyses will require particular statistical and computing expertise. We started during a Master training (Justine Léauté) that I coordinated with the naturalist association (**Baeta, Léauté, Sansault & Pincebourde in prep.**). We analyzed the influence of landscape structure around water bodies on the community structure of Odonates (including both dragonflies and damselflies). The main striking result is that we identified the distance within which the surrounding terrestrial areas clearly influence the communities of Odonates in water bodies: up to 800 m for Anisoptera. This distance was constant whatever the type of landscape (forest, agricultural fields, and urban structures) but was smaller and variable for Zygoptera. This result has important implications for the conservation biology of these keystone aquatic species.

The PRAO did a particular emphasis on the species *Leucorrhinia caudalis* which at that time (2012) was spotted on the IUCN Red List as threaten species. One of the actions we proposed for this species focused on the dispersal ability of the immature stage. After the adult emerges, it flies away and leaves the aquatic system for about 10 days to mature sexually. The distance traveled and the microhabitats used for maturation were undetermined. We used passive telemetry system to follow immature individuals with a radar (**LeNaour, Baeta, Sansault, Deville & Pincebourde 2019**). Immatures were equipped with a passive diode that reflects a signal coming from an emitter (Figure III.27). We found that immature individuals do not fly far away from the pond. We discovered that they fly towards the top of the oak canopy surrounding the water body during their maturation before they come back to the aquatic system. This observation indicates that the dragonfly establishes a trophic link between the aquatic and terrestrial systems. The immature likely feeds on insects including aphids or flies at the top of the canopy. However, we also highlighted the difficulties of applying the telemetry to conservation issues. Despite much progress recently, telemetry remains challenging when it comes to study relatively small species.



**Figure III.27.** Illustration of two immature individuals (*Leucorrhinia caudalis*) equipped with the diode system. Individuals were marked on the wings to identify them when they were detected. Photographs: Eric Sansault.

The field of conservation physiology is now rising at a spectacular rate (e.g., the new excellent journal *Conservation Physiology* already has a high impact factor after only few years). We measured and analyzed the relationship between water temperature heterogeneity across water bodies and the spatial distribution of emerging dragonflies (see above). These microclimatic patterns should now be compared with physiological measurements on Odonate larvae to quantify the influence of water temperature variations on the physiological performance of the dragonfly larvae. Three parameters need to be collected: the temperature dependency of metabolic rate, the thermal limit (CT<sub>max</sub>) and their preferred temperature. The influence of dissolved oxygen on these thermal traits will also be determined. We recently equipped our laboratory (INOV team) with several high technologies to measure these traits, in particular a shuttle box for thermal preference and a microplate allowing the measurement of oxygen consumption of individual larvae and even eggs (Loligo systems). We expect these measurements to be informative for conservation biology of dragonflies. Water bodies could be managed to adjust water temperature so it matches the favorable temperature range even in a changing climate. Such management includes the provision of large vegetation (both aquatic

and terrestrial) to provide shade at least over a portion of the water body or the management of the slopes of the pond to install an important temperature gradient to permit thermoregulation for the larvae. The type of aquatic vegetation should also matter for the thermal heterogeneity of the water body, and most importantly for the management of dissolved oxygen in the pond.



# *Part IV.*

## Research perspectives

*This section gives a synthetic view of my research perspectives over the short, medium and long terms.*



The larva of the dragonfly *Cordulegaster Boltonii*. © Urft Valley Art.



Instead of classifying my research perspectives according to short, medium and long-term research ideas, I choose to rank them by topic to better illustrate the directions I would like to take in the future. A rough calendar is given to illustrate the feasibility and to explain which projects will necessarily imply collaborative work either with students or with other researchers. My research perspectives follow two paths that are developed below:

- Expanding the microclimate approach to other biomes and microhabitats, and in particular compare terrestrial and aquatic systems to better comprehend the relationships between microclimatic patterns in the field and the thermal biology of ectotherms;
- Integrating the ecology of wind into the frameworks of ectotherm vulnerability to climate change: how wind fluctuations and changes can annihilate potential acclimation to, or tolerance of, stressful environmental conditions, or by contrast will air flow help ectotherms survive future conditions by decreasing their body temperature?

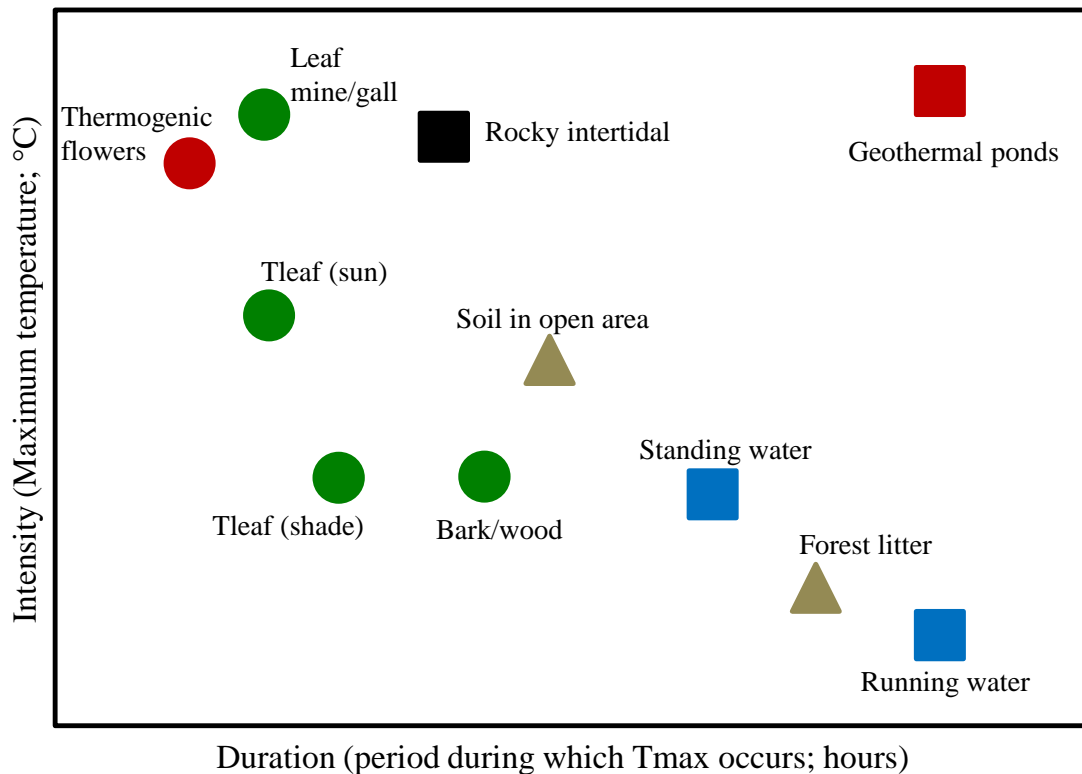
## 1. Thermal ecology across biomes

### *a) Microclimates should influence the way we measure thermal limits*

Thermal biology studies provide crucial knowledge to estimate and predict the vulnerability of ectotherms to global changes. In particular, the thermal limit of organisms can be used later by macroecologists to ‘map’ the vulnerability of organisms across the world and to infer where organisms are more vulnerable to warming (Sunday et al. 2019). One major drawback in this macroecological approach however is that these thermal limits are taken from the literature as they come, and these traits are often measured using quite different temperature assays. This is an important limitation. Thermal limits are well known to vary largely depending on the starting temperature and the rate of increase during the experimental run (Terblanche et al. 2011). Researchers called for a coherent and standard way of measuring thermal limits of ectotherms, so we can compare these limits among and between species (Jørgensen et al. 2019). It is indeed important to have the same experimental design for comparative physiological studies (e.g., to compare the acclimation abilities or phenotypic plasticity among species). However,

if these thermal limits are used to infer vulnerabilities to climate change, I argue that the temperature assays should reflect the temperature conditions that the organism experiences in the field. Therefore, thermal limits should be measured using *different* experimental designs depending on the microhabitat characteristics. A more appropriate standard design could include different habitat-specific sets of values for thermal parameters such as rate of increase and starting temperature.

In this context, the microclimate of ectotherms could be defined with a minimum of three parameters: the (maximal) daily rate of increase in temperature, the maximal microclimate temperature reached during the day and the time spent daily at this maximal temperature. These metrics can be taken as averages across growth season or during the hottest part of the year, or the maximal levels can be extracted from microclimate temporal series. As I illustrate below, different microhabitats in different biomes likely show contrasting values for such parameters (Figure IV.1). The relationship between intensity and duration of the thermal stress in the natural microhabitat of a species should define the temperature trajectory of thermal assays designed to measure thermal limits. A thermal limit measured at unrealistic parameters is (almost) useless in the context of warming impact predictions. I propose to determine the error in predicted thermal safety margins under climate change depending on the way thermal limits are measured by comparing different designs with parameters that are more or less close to realistic patterns measured in the microclimate of the species. I will probably tackle this problem on a plant-herbivore system for which we have the most comprehensive knowledge on microclimate and thermal biology (lizards can also be an excellent model for this project). Further, we could also estimate the error in predictions of warming-induced species distribution shifts' as function of the temperature assay used to determine thermal limits. Collaborations with macroecologists will be necessary at this point.



**Figure IV.1.** 'Exposure' diagram showing the relationship between the intensity of daily temperature (e.g., maximal temperature that can be reached during the growing season) and its duration (e.g., the time daily during which this temperature applies) for several types of microhabitats: plant-associated (circles), water-related (squares), and soil (triangles) microhabitats.

The three parameters used above to define microclimates are expected to strongly vary across different microhabitats. For instance, an aphid at the surface of a tree leaf exposed to full sun experiences a rapid increase in temperature during the day as radiation load increases and ambient air warm up, up to a relatively high maximal leaf temperature that could remain stable for an hour or so, before it starts to drop down in the afternoon. By contrast, a wolf spider at the surface of the forest litter lives in a thermal environment changing slowly during the day, and with a relatively low maximal surface temperature due to the forest cover buffer (De Frenne et al. 2019). Therefore, the aphid experiences rapid warming with intense but short thermal stress while the wolf spider gets slow warming with mild but long exposure to (potentially) stressful conditions. Different microhabitats and biomes can be ranked this way according to intensity of the thermal stress (e.g., daily maximal temperature) and to the daytime period over which this temperature applies (Figure IV.1). On one hand of the spectrum, thermogenic flowers and the surface of (temperate) leaves in the sun expose organisms to relatively high maximal

temperatures lasting no more than 1 or 2 hours during the day (Figure IV.1). By contrast, forest litter and aquatic microhabitats are among the most buffering habitats, exposing ectotherms to lower maximal temperatures but those are operating over several hours during the day (Figure IV.1). In this diagram, the top-right corner gives the most challenging environments for life (i.e., high maximal temperature lasting days or months), like geothermal ponds (e.g. in Yellowstone) in which particular bacteria but also few species of dragonflies can develop (Schott & Brusven 1980; Dunckel et al. 2009). Note that this diagram alone cannot be used to assess the vulnerability of ectotherms to warming because these patterns have to be integrated later with the thermal limits of organisms (Pincebourde & Casas 2015, 2019). This ‘exposure’ diagram is proposed to identify the conditions that should be applied in temperature ramping trials to measure these thermal limits.

I propose to analyze these patterns for as many microhabitats as possible (the diagram in Figure IV.1 remains qualitative if not speculative for the moment). A first step would be to retrieve published microclimatic data to extract the different parameters that define the microclimate in this context. I will of course complement with my own microclimatic measurement that I have collected so far, and also with data I could collect in the future on specific microhabitats. For example, urban microhabitats may be integrated in such a database. This analysis will generate guidelines for measuring appropriately thermal limits of ectotherms in these different microhabitats. This approach was included in a proposal submitted to the CESAB call for project in 2014 and 2015, but the project was not successful. Macroecologists are however quite demanding and calling for such microclimate database (Bramer et al. 2018).

*Scientific strategy:* I will develop this project over the medium term in the next 5 years. The logistic difficulty lies in the multiple systems that need to be ‘sampled’, although I already have worked with most of them (leaf surfaces, leaf mines and galls, freshwater, rocky intertidal, forest litter). Clearly, the support of students and collaborators will be necessary to complete such project. I will certainly have to fund this project from multiple sources: different grants can cover each of the main systems involved here. Collaborations will play a key role, and a national/international network for microclimate ecology could emerge from this approach.

*b) Hot flowers: influence of plant thermogenesis on pollinator's thermal biology*

As shown in the 'exposure' diagram above (Figure IV.1), thermogenic plants can generate intense but fleeting thermal conditions for the insects that visit flowers. A variety of plants have flowers that produce heat to warm up all or some parts of the flower (Seymour & Schultze-Motel 1997; Seymour et al. 2003). The exact function of thermogenesis in plants is not always entirely clear and several hypotheses have been proposed (Ervik & Barfod 1999). For example, insect pollinators can benefit from visiting such flowers, by saving energy for activity at night when ambient temperature is lower than inside the flower (the heat reward hypothesis). Insects therefore stay longer within the flower thereby increasing the probability to get fertilized. This function was illustrated in a tropical *Arum* pollinated by beetles: temperature within the flower at night was optimal for the metabolism of the beetles during their reproduction activity (Seymour et al. 2003). In this system, the heat produced by the flower plays an important role in stabilizing the positive interaction between the plant and its pollinator.

However, not all thermogenic plants have such reciprocal positive interaction. Temperate *Arum* species, including *Arum maculatum* and *A. italicum* which are widespread in France, produce heat to attract insects and trap them in a compartment of the flower for a day before they are released to allow them to visit other flowers, favoring pollination. The plant exploits these insects by first attracting them (the heat produced is thought to increase the emission of the odor that attracts flies) and second by trapping them (via the use of hairs that create one-way paths during a short time) (Albre et al. 2003; Chartier et al. 2016). The influence of the flower microclimate on the thermal biology of the insects has never been studied in this system. The flies of the genus *Psychodidae* (Diptera, Nematocera), and in particular the species *Psychoda phalaenoides*, are the main insect attracted and exploited by these *Arums* (Chartier et al. 2013). In this small fly, the female normally lays eggs in fresh cow dung pads and the semi-aquatic larvae complete their cycle in these dung pads. These flies may therefore be lured by the plant when it 'mimics' the temperature of a cow dung pad. But the plant should be cautious to not overheat the flies: strong selection pressure against plants that produce too much heat is expected.

I propose to compare the thermal limits of the *Psychoda* flies with the temperature patterns of the *Arum maculatum* flowers. Preliminary measurements

suggest that Arum flowers can be more than 15°C warmer than ambient (Figure IV.2), and up to temperatures >35°C. The thermal biology of *Psychoda* flies is totally unknown but I speculate that a thermal limit above 40°C is unlikely for such flies active in May at temperate latitudes. It is therefore possible that the flies meet conditions near their thermal limit in the flower of Arums. Another novel aspect of the interaction that is worth studying is the daily rhythm of the plant thermogenesis relative to the daily activity window of the flies. Arum flowers are producing heat only late afternoon and for 2-3 hours. Attraction of the insect should be effective only if these insects are actively flying at that time of the day, a trait that was never quantified in these species. Moreover, I have preliminary data indicating that the environmental conditions (temperature, light, soil moisture) can induce a shift in the time at which heat is produced by the flower. For example, higher ambient air temperature causes the flower to emit heat earlier during the day by several hours, leading to higher flower temperatures. It is not known if *Psychoda* flies are active in the middle of the day when ambient air temperature are abnormally high in May such as during heat waves. My hypothesis is that heat wave events will induce a mismatch between the plant thermogenesis and the insect activity window, thereby disrupting the strategy of the plant and rendering it inefficient for pollination. In addition to this project, in collaboration with Dr. Olivier Dangles (IRD) and Marc Giberneau (Univ Corse), we will develop a similar approach for a thermogenic palm tree in Ecuador (see [Pincebourde et al. 2016](#)). The comparison between a temperate and a tropical thermogenic plant would provide an indication on how the environment influences the evolution of thermogenic function in plants.



**Figure IV.2.** Production of heat by the flower of *Arum italicum* near Tours (France) during Spring. Heat production by the spathe is supposed to increase volatile emission and/or to increase detection by pollinators.

*Scientific strategy:* I did include these ideas in a proposal submitted to ANR in 2017, but it was not funded. In the near future (2019/2020), I will propose this project to obtain a PhD grant at the University of Tours. All the equipment necessary for this project are already available at IRBI. This project could launch a junior scientist on the topic of effects of climate change on daily activity rhythms of plants and insects and their interaction. In parallel, I will participate to the development of a project (ANR) on the palm tree in Ecuador led by my colleagues.

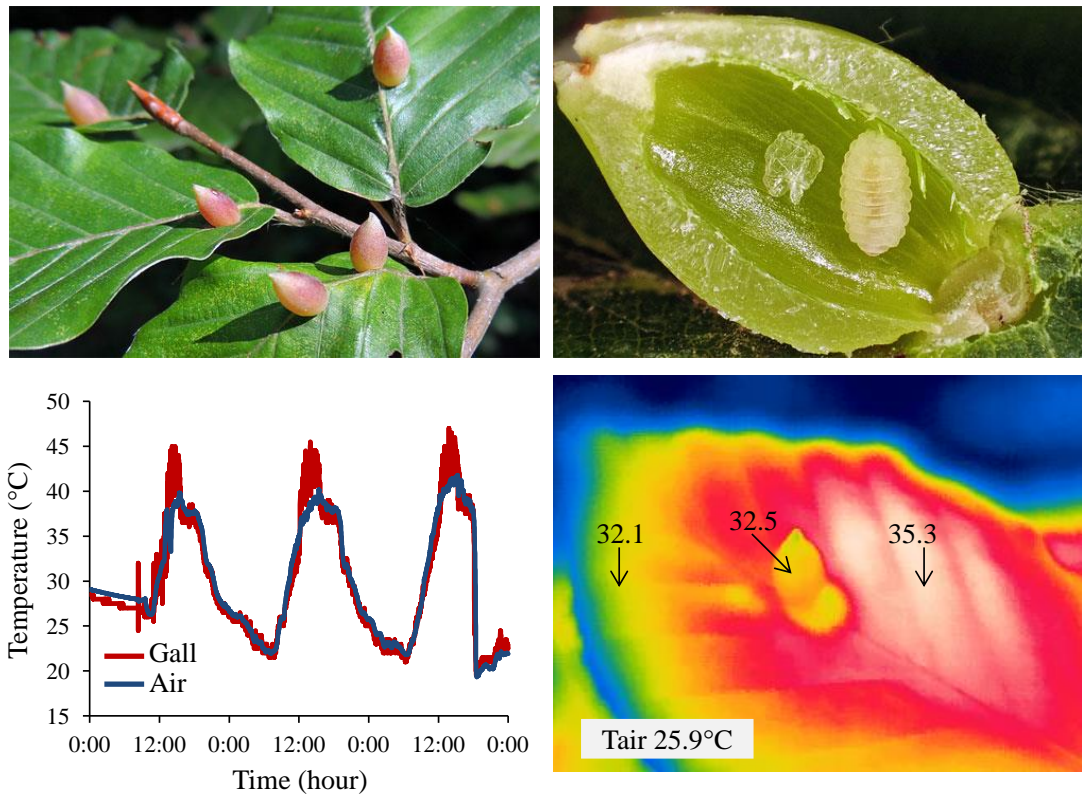
*c) Hot galls: interaction between temperature and oxygen in plant galls*

I will continue to look closely at very small structures developed by insects on plants. My previous works on apple leaf miner suggest that the atmosphere within leaf mines (less than 1 cm<sup>2</sup> area) can reach temperatures more than 12°C above ambient air during a short period of time during the day (e.g., [Pincebourde and Casas 2006, 2015](#)). Nevertheless, it remains unknown if this “inside is warmer” rule can be generalized to the many different structures that insects can develop on plants: insect galls, borers and leaf tiers. As I show in the sections above, a complete understanding of the microclimate conditions within these structures is key to better



comprehend their thermal adaptations and their potential responses to climate change.

Leaf galls are an interesting model in this context because the high diversity of shapes, sizes and coloration (Stone & Schönrogge 2003) should induce large variations in temperature inside galls. Amazingly, the literature reporting temperature within galls is extremely limited (Layne 1993). Moreover, based on a theoretical model of gas diffusion across gall tissues, we predict that oxygen limitation should arise for large galls and/or under certain circumstances like at high temperature (**Pincebourde and Casas 2016**). In some ways, gall inducers may have limited thermal tolerance due to hypoxia, as it happens for some aquatic macroinvertebrates (Verberk et al. 2016). Therefore, in the near/medium term future (a project started in 2019), I will initiate projects on the temperature and oxygen conditions in plant galls, how these conditions depends on gall morphology, and the thermal adaptations in these insects. My hypothesis is that large galls (e.g., large galls induced by cynips on oak) should reach higher internal temperature than small galls (e.g., galls on beech; Figure IV.3), but at the same time they should get hypoxic conditions when photosynthesis in gall tissues is low (which is likely to happen at elevated temperature and during the night). Therefore, insects inducing large galls may have lower thermal limits than insects developing in small galls, making them more vulnerable to environmental warming, contrasting with the intuition that a large gall would better protect its inhabitant from environmental hazards.



**Figure IV.3.** The beech leaf gall (*Mikiola fagi*) is found at the upper surface of beech leaves and therefore they can receive direct solar radiation. The larva is living inside a relatively large space inside the gall, with a thin wall, which explains the normoxia. The temperature inside this air space can deviate strongly from air temperature in particular when it is hit by solar radiation (the graph shows the temperature trace of a single gall during 3 days corresponding to the intense heat wave we had in July 2019 in Europe). The surface of the gall can be much warmer than ambient air but still remains few degrees cooler than the warmest portion of the leaf surface. The infrared image nicely illustrates why this galler is sometimes called the 'lemon gall'. Photos at the top: bladmineerders.

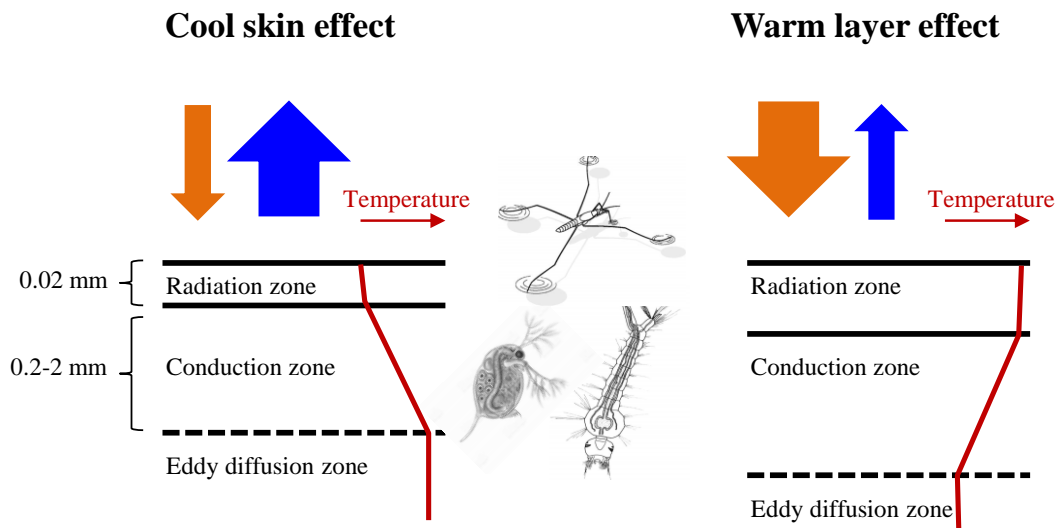
**Scientific strategy:** Such a comparative approach will inevitably take several years depending on success rate to be funded and to enroll students. I started in 2019 with the impulse of a collaborator (Prof. John Terblanche, Stellenbosch University, South Africa) to work on these issues in galls induced by *Mikiola fagi* (Diptera: Cecidomyiidae) on beech (*Fagus sylvatica*). The first measurements indicate that hypoxia does not occur in these small galls, the internal temperature of which can be  $>5^{\circ}\text{C}$  higher than ambient. By contrast, hypoxia can be severe in the large galls of the hymenopteran *Cynips quercusfolii* which induces spherical galls on oak (*Quercus*).

*d) Microclimate gradients at finer scales*

The leaf microclimate represents the interface between plant tissues (with specific abiotic conditions in the inter- and intra-cellular spaces) and the free atmosphere. As I showed in my recent research activity, tiny arthropods living at this interface experience particular thermal environments that drive their thermal adaptation (**Pincebourde & Casas 2019**). Thus, the idea that interfaces are heterogeneous enough at fine scale to generate diverse thermal adaptations can be expanded more widely to other systems (following the general guideline in Figure IV.3). In the future, I would like to focus on one of the most amazing life interface: the air-water interface, and ectotherms living at this interface either at the air or the water side. This air-water interface is of interest not only in terms of thermal environment but also in a context of multifactorial environments because dissolved oxygen is likely to vary at fine scale within this interface (on the water side). Nevertheless, almost nothing is known on the thermal conditions at the air-water interface and the thermal biology was studied only in very few ectotherm species that use this interface.

From a biophysical point of view, the interface between air and the water of a (still) pond is expected to allow the development of a temperature gradient (Figure IV.4), which was measured to range between one and several degrees within the first 2 mm of water layer in lab settings (Hill 1972; McKeown et al. 1995) but remains unknown in natural conditions. The surface of the water receives large amount of incoming energy during the day (solar radiation) which should warm up significantly the first millimeter layer of the water. This warm water may not significantly influence insects living on the water surface, in the air. These aerial insects receive solar energy and they are relatively protected from convection losses by being embedded within the pond boundary layer. On the other side, aquatic organisms living below the air-water interface can be influenced by this thin layer of warm water, especially because the heat budget of aquatic organisms is mostly driven by conduction. They can however move up and down by few millimeters to escape these conditions at the interface. Under some circumstances (high air-water thermal difference for instance), a 'cool skin' effect can develop wherein the first mm of water is cooler than the bulk of water below because of high latent heat loss (McKeown et al. 1995). Conditions at the interface can change depending on other factors such as the development of a bacterial mat, which may modify the conduction

of heat downward and the absorption of solar energy. Wind is also expected to homogenize the conditions at the interface by favoring Eddy mixing (Hill 1972). In terms of thermal biology of ectotherms living in this interface, my hypothesis is that the thermal limits of ‘aerial’ arthropods (on the surface) should be higher and more plastic than those of aquatic ectotherms (below the surface) because the later can easily escape the heat by moving vertically even over quite short distances (mm/cm scale). Nevertheless, dissolved oxygen may play a role in the vulnerability of these aquatic ectotherms, although hypoxia should be intense enough to induce a decrease of thermal limits.



**Figure IV.4.** Thermodynamic zones in the air-water interface (inspired from knowledge on the air-sea interface; McKeown et al. 1995; Fairall et al. 1996). In the cool skin model, evaporative heat loss (blue arrow) surpasses the radiative heat gain (orange arrow) such that the first layers are cooler than the water body below. In the warm layer model, by contrast, the radiative heat gain is more important than the latent heat loss and the thermal gradient is reversed. These models apply to steady conditions. Wind speed and water current are expected to mix these layers thereby annihilating the temperature gradients. The size of this thermal gradient scales with the body size of most tiny macroinvertebrates that use this air-water interface.

This project at the air-water interface could be supported by the development of a new structure that started very recently (2019) in the context of conservation biology. I have been collaborating with the naturalist association ANEPE Caudalis (Baeta, Sansault & Pincebourde 2012) since 2011 to understand the drivers allowing the maintenance of populations of dragonflies and damselflies, in particular

for threatened species. In 2019, we had the opportunity to propose the development of a new structure based on basins that were previously built and used by a fishery that does not exist anymore. Several facilities in the world already propose aquatic mesocosm with varying degrees of controlled parameters and diverse measured factors (there are at least 55 facilities in Europe when combining stream, lake and pond ecology<sup>1</sup>). The originality of our system will be related to its location near a source of more than 40 Odonate species. Source/sink processes are an important component in population biology and in conservation biology. In this system, we will be able to study how Odonate species successively colonize new sites and how females make their choice as to where to lay eggs according to environmental parameters and to properties of the air-water interface. Such question is particularly crucial in the context of climate change and water management: can we develop engineering strategies to make aquatic systems resilient to climate change? How can we manage aquatic systems to increase the ability of microhabitats to buffer part of environmental warming and to allow species to survive? In this context, we envision to set factors in the basins such as environmental architecture (3D complexity of the vegetation and varying slope of the substrate) and physical quality of water (by controlling water temperature and dissolved oxygen). Such studies will include eco-physiological measurements on Odonate larvae for which we have little knowledge compared to adults.

*Scientific strategy:* Aquatic ecology is and will continue to take a significant part of my research time. This (medium to long term) project will be linked to the grants I will prepare on conservation biology. Therefore, I see this air-water interface project more as a side project, involving students, embedded in a larger project focusing on the conservation biology in aquatic systems.

e) *Terrestrial versus aquatic microclimates*

Terrestrial and aquatic microhabitats show distinct thermal signatures with inevitable consequences for the thermal biology of ectotherms. The thermal variance is high in most terrestrial habitats (there are exceptions) and relatively low in most freshwater environments (again, there are exceptions). The spatial heterogeneity also

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<sup>1</sup> See: <http://mesocosm.eu/facilities/>

differs between terrestrial and aquatic habitats, with temperature gradients that occur with different amplitude. Another idea behind the ‘exposure’ diagram in Figure IV.3 is to study the impact of these variance patterns on the evolution of thermal biology traits in ectotherms. The plasticity of thermal limits might depend on this level of variance. Indeed, in general, terrestrial ectotherms show a rather limited plasticity in their thermal limits (Araujo et al. 2013; Gunderson et al. 2017). By contrast, the thermal limit of aquatic invertebrates seems to be relatively more plastic (Chown et al. 2015). This counter-intuitive observation may be explained by the temperature heterogeneity occurring at fine-scale. From my experience, aphids or spider mites have to move at the leaf surface over only few centimeters to change their body temperature by about 10°C while a dragonfly larva would have to swim over several meters to experience a similar change (if possible at all). This observation is coherent with a behavioral inertia (Gunderson & Stillman 2015) that would then be larger in terrestrial than aquatic habitats.

In addition, preferred temperature and acclimation ability could be plastic only within a given range of thermal variance because acclimation cannot be possible when the environment changes rapidly, or cannot be beneficial if it changes only slowly. Behavioral thermoregulation is an important driver of how fast ectotherms respond to climate changes but the level of plasticity of their preferred temperature should determine the fitness consequences of behavioral thermoregulation in a changing environment. My preliminary study on the preferred temperature of *Drosophila* at larval and adult stages indicate that this trait can be hyper-plastic in response to different environmental challenges. This hyper-plasticity would allow the insect to react quite differently during behavioral thermoregulation with quantitative consequences on the overall response to a changing environment in terms of fitness. I would like to pursue this topic. An important question is to what extent this hyper-plasticity is adaptive, and how it could boost adaptation to climate warming, depending on the physiological mechanisms involved. I will start to work on this question in collaboration with a new Maitre de Conférence recruited recently in the group (Dr. Vincent Foray). This project will necessitate multiple measurements of thermal traits across species and across terrestrial and aquatic biomes (Figure IV.3). The team INOV has acquired several equipments these past years that will enable routine experiments in both media (including metabolic rate of single small



individuals as function of temperature, preferred temperature, thermo-limit respirometry).

*Scientific strategy:* This comparative analysis between aquatic and terrestrial microclimates is my priority in the short term. I will start writing a proposal in 2019/2020, especially for the next BIODIVERSA call for projects on biodiversity and climate change. This project will be a great opportunity to strengthen the position of our team INOV at IRBI in the field of thermal biology in particular with Prof. Claudio Lazzari and Prof. Jérôme Casas. My vision is to use this project as a structuring unit for part of our team INOV: the couple [thermal variance - thermal limit] can be measured on several organisms that are studied otherwise in the team, and equipments will be jointly developed and used.

*f) Towards geographical gradients of microclimates?*

Measuring the gradient over latitude and/or altitude is a natural and logical approach for most of the projects I describe above because it allows to study the dynamics of a system across a range of environmental conditions and on populations that are adapted to different conditions. General concepts such as environmental stress gradient or climate variability hypothesis could then be tested. I see two opportunities to inter-connect my fine-scale approaches with macroecological processes.

First, I would like to do more on the latitudinal gradient of leaf surface temperatures and the extent to which it explains a geographical gradient in thermal limits of herbivore insects. This project follows our work published in PNAS in 2019, and also the work accomplished by my PhD student Robin Caillon. I will study tree leaf temperature patterns along a latitudinal gradient including tropical, sub-tropical and temperate areas. With such a board latitudinal gradient, a community approach is naturally the most pertinent. Several tree species should be sampled at each site, and different arthropod communities will be collected and tested for their thermal limits. The major constraint will be to access the top of the canopy to both deploy dataloggers measuring leaf surface temperatures and to sample arthropods. Amazingly, specific systems allowing a direct access to the forest tree top are much more present in the tropics than in temperate zones. An alternative would be to use



remote sensing technologies to estimate canopy surface temperatures but this approach does not allow estimating microclimate temperatures in the vertical gradient between the soil up to right below the canopy surface ('arborality' concept; Scheffers et al. 2017). Our Institute IRBI has initiated a project in 2019 to acquire and deploy mobile tower crowns equipped with fancy systems to measure, for instance, physical and ecophysiological variables at any point within a tree canopy, focusing in particular on large oak forests (25-30m height) which are suffering from warming. I currently contribute to the development of this project which includes a large consortium at the regional scale (Région Centre, to be potentially funded by the CPER).

Second, the microclimate temperature pattern within different microhabitats could have a latitudinal/altitudinal gradient that vary in its shape, amplitude, and range. The best example in the literature is the patchy latitudinal gradient of mussel body temperatures in the rocky intertidal (Helmuth et al. 2002) versus the absence of geographical gradient in the ability of forests to buffer atmospheric temperature extremes (De Frenne et al. 2019). However, such examples remain rare. In particular, terrestrial and aquatic microclimates are expected to be linked to latitude/altitude in a different fashion. The idea is to test the relationship between the intensity and duration of the thermal stress in various microhabitats (see Figure IV.1) across latitudes. Some microhabitats may be good buffers within a given latitudinal range, but could also perform poorly otherwise. We lack data (or a meta-analysis remains to be done) to draw specific hypotheses for each type of microhabitat. Interestingly, forest covers buffer atmospheric warming with the same amplitude across latitudes and forest types or dominant tree species (De Frenne et al. 2019). Nevertheless, this study still is at a coarser scale (air temperature about 2 m above forest litter) than what I envision to study.

*Scientific strategy:* I envision the use of the COPAS system in French Guiana (CNRS field station) to sample tree leaf temperatures and arthropods at the top of the tropical rain forest. A project was developed in 2019 in collaboration with Prof. Arthur Woods and Prof. Michael Dillon. Part of the research on latitudinal gradients should be included in the next BIODIVERSA call for projects on biodiversity and climate change (led by Aurélien Sallé at the Univ Orléans). Most of the ideas reported in this section are however quite large and will require significant funds and partners. A

system to access and measure physical and ecophysiological variables within forest canopies will also be developed by the consortium of researchers working on forest insects in Région Centre: I will contribute to this development led by our Institute.

## 2. Wind ecology: integrating air flow variations at microscale

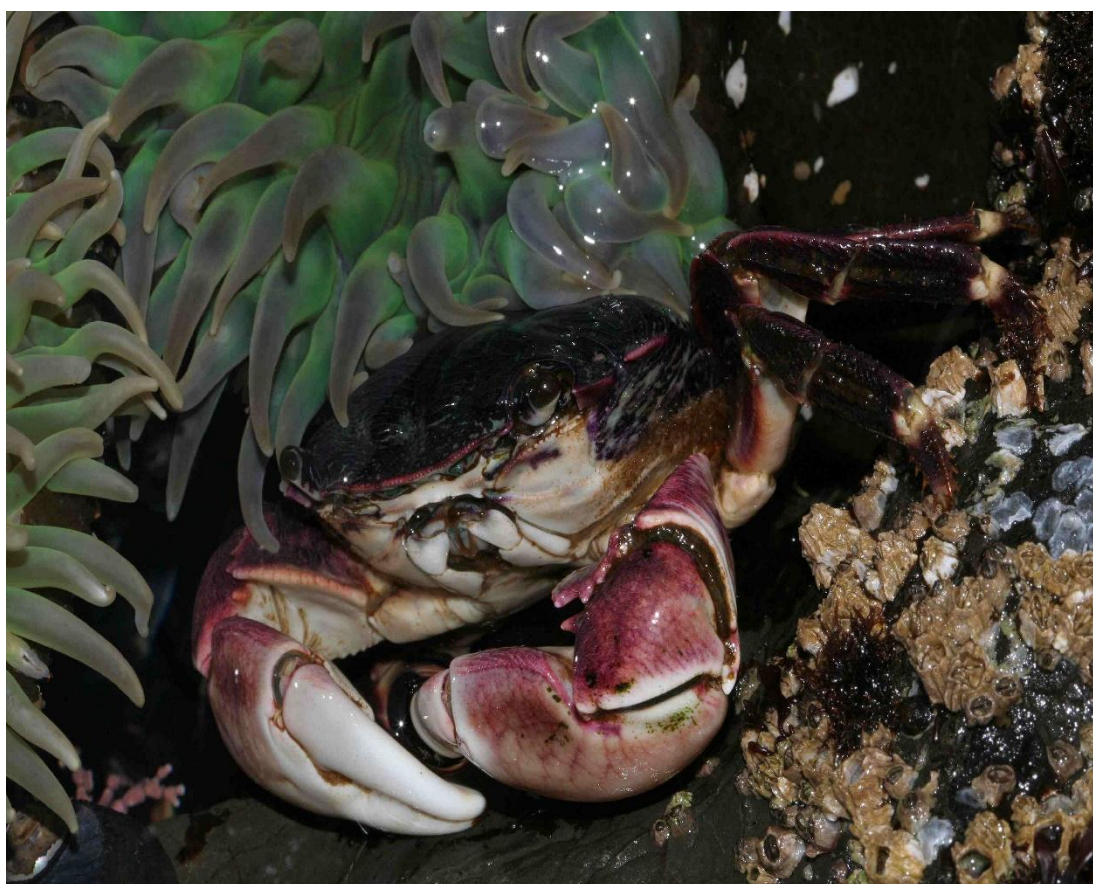
Wind is another abiotic factor that matters for living organisms. Its importance was demonstrated for long distance dispersal of seeds for instance (Nathan et al. 2002). Wind speed also has a high impact on the heat budget of organisms (Gates 1980). As a consequence, wind speed is necessarily included in biophysical models of heat exchange. Often, wind speed is provided as an average over time at the hour or daily temporal resolution, depending on the temporal scale of the heat budgets. This is practical (I did the same in my own research) mostly because I feel like we do not really know exactly how to handle the extremely high frequency at which wind speed varies in the natural environment. Wind speed can vary tremendously at the second and minute scales (Vogel 2009). This is especially true for wind speed around objects in the environment such as in plant canopies for instance. Technology allows measuring wind speed at the second time step. But what is missing is the extent to which this frequency of fluctuation matters for organisms, and if so, what is the amplitude of its effect on biological processes. In the long term (>10 years), I would like to start working on these issues that I detail below. These ideas require new expertise that I do not have now. Specific training will be necessary during the next 5 years to be prepared for this new topic. Such approach requires knowledge on fluid dynamics and turbulent flows in plant canopies (Finnigan 2000) at finer scales than usually done in fluid dynamics studies in forest canopies.

The first topic directly interconnects my research on the leaf temperature and the biophysical ecology of wind. Logically, the heat budget of a tree leaf should be computed using the wind speed value recorded near the focal leaf. Usually, wind speed in plant canopies is modeled following an extinction coefficient depending on the density of foliage across the wind speed vector, which again supposes a laminar flux (e.g., Sinoquet et al. 2001). Therefore, I would like to deploy tens of wind speed loggers capable of measuring high-frequency fluctuations across tree canopies

differing in their architecture to assess the wind speed gradient complexity in plant canopies. Then, I can compute the heat budget of leaves based on these high-frequency measurements versus average wind speed for laminar flows to estimate the bias induced by neglecting these high-frequency variations of wind speed and turbulent transport. Another aspect is related to the ecophysiology of the leaves: the opening level of stomata, which matters for leaf surface temperature, may react differently to highly fluctuating wind speed patterns compared to the average wind speed value. For example, frequent (every minute) but fleeting (just 5 seconds) puffs of high velocity air flow should suddenly decrease leaf surface temperature, inducing stomata to be more open than when exposed to the average wind speed value which remains low, causing elevated leaf surface temperature and stomatal closure. I expect different biological consequences depending on the arthropod species like the spider mite (which can thermoregulate behaviorally at the leaf surface) versus some aphids (which do not move a lot and instead endure the conditions where they sit). Even more complex interactions can be imagined because the mass of insects at the leaf surface induces changes in leaf fluttering frequency during wind-plant physical interactions (Kothari & Burnett 2017).

*Scientific strategy:* The team INOV already has some equipment allowing air flow visualization and determination of flow velocities at surfaces (e.g., PIV, high-speed cameras). Therefore, this long-term project matches the objectives of the team and its philosophy on physical ecology, in collaboration with Prof. Jérôme Casas and Dr. Thomas Steinmann in particular. Strong collaboration with colleagues at INRA PIAF (Dr. Marc Saudreau) will also be helpful, as well as with other teams in France that work on turbulences above and in forest canopies.

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Life in the rocky intertidal in Bodega Bay, California. During my postdoctoral studies, I was astonished by the diversity of strategies developed by intertidal organisms to survive one of the harsher habitats in the world. Photo: Sylvain Pincebourde.

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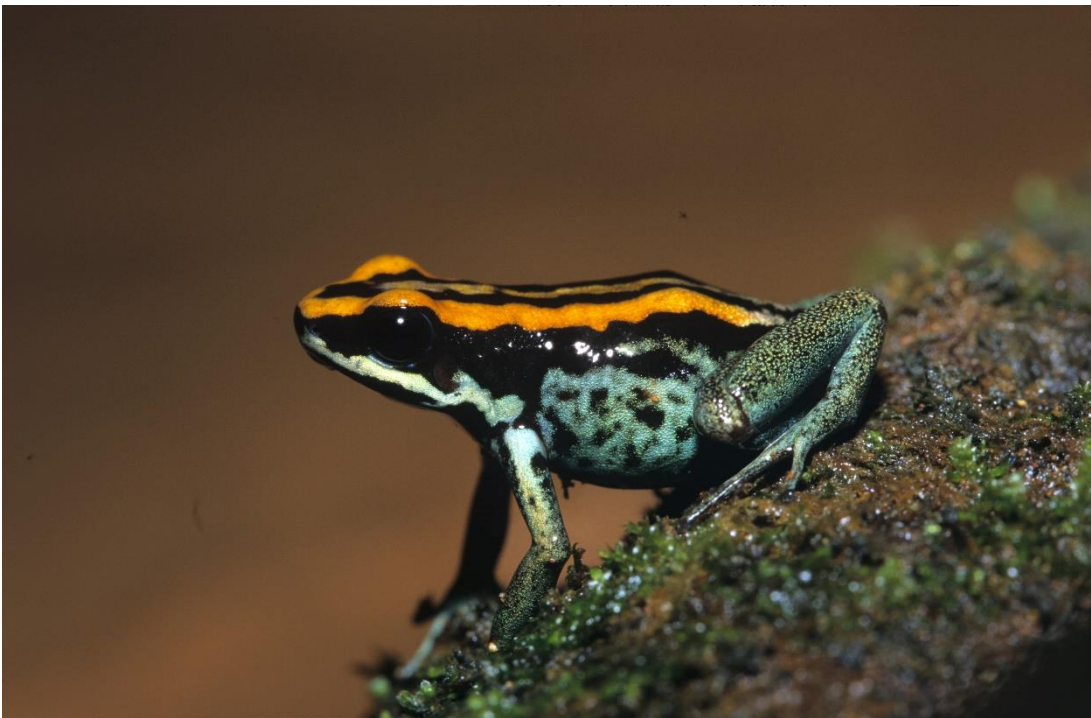
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# Appendix 1.

## Synthèse en français

*Ce rapport d'HDR étant rédigé en anglais, cette synthèse écrite en français est ajoutée conformément au règlement de l'Université de Tours.*



La grenouille *Dendrobates vittatus*, l'une des quelques espèces de dendrobates du Costa Rica, apparition surréaliste dans le sous-bois tropical. Photo: Sylvain Pincebourde.



## ÉCOLOGIE THERMIQUE DES ECTOTHERMES: Rôle du microclimat dans la réponse au changement climatique

Cette synthèse en français présente brièvement (1) mon activité scientifique, (2) mon implication dans l'enseignement, la formation et la diffusion, et (3) mon rôle dans l'encadrement, l'animation et le management de la recherche.

### 1 – Mon Activité Scientifique



*Figure A1.1. Schéma synthétique de mon activité scientifique.*

#### 1.1 Introduction : mes orientations thématiques

Mes recherches se focalisent sur le rôle du microclimat des organismes dans leur réponse aux changements environnementaux. Mes approches intègrent l'écologie, la physiologie, et la biophysique sur des modèles biologiques très variés (insectes, acariens, échinodermes, plantes) et dans différents milieux (marin, terrestre, aquatique). Mes recherches s'appuient sur une observation très simple : les organismes vivent souvent dans des microhabitats au sein desquels les conditions

abiotiques peuvent différer des conditions dites atmosphériques (i.e., celles mesurées par nos stations météo). Ainsi, un acarien à la surface d'une feuille au soleil rencontre des températures de plusieurs degrés au-dessus de la température ambiante, ou encore une larve d'insecte aquatique vit dans une eau au régime thermique distinct de la température atmosphérique. Cette notion de microclimat n'est pas nouvelle, et apparaissait même déjà dans la théorie de Darwin. Pourtant, aujourd'hui, cette notion de microclimat est intégrée dans les modèles prédictifs des impacts des changements globaux sur la biodiversité de façon marginale seulement. La principale raison est que les conditions microclimatiques sont méconnues pour une vaste majorité d'organismes – en particulier pour les petits organismes tels que les unicellulaires et les arthropodes.

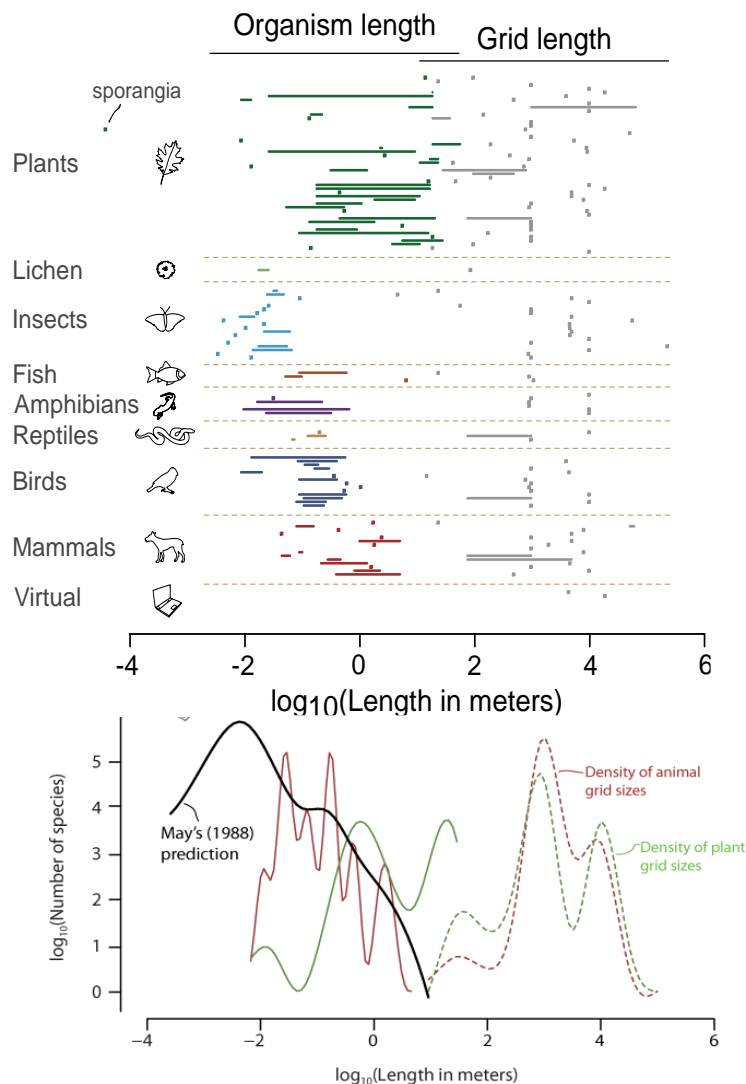
**Mon objectif général** est de comprendre les mécanismes sous-jacents à l'impact du microclimat sur l'écologie thermique des organismes et sur leur capacité d'adaptation aux changements de température. Cette question générale a nécessité des développements conceptuels. Plus particulièrement, un problème d'échelle spatiale se pose : à quelle échelle un organisme échantillonne-t-il son environnement thermique ? (**section 1.2** ci-dessous). Ma vision n'est pas d'inventorier les conditions microclimatiques, mais plutôt d'échantillonner dans différents types d'habitats ayant à priori des patrons microclimatiques différents et d'étudier leurs effets sur l'écophysiologie des organismes ectothermes vivant dans ces milieux. **L'hypothèse globale testée est que les organismes doivent avoir un potentiel adaptatif d'autant plus important que les conditions microclimatiques varient avec une haute fréquence.** J'ai ainsi travaillé sur différents microclimats : le microclimat foliaire (**section 1.3**) qui présente la particularité d'être généré et modulé par un être vivant, le végétal ; la variabilité microclimatique au sein de la zone d'estran (zone de balancement des marées, **section 1.4**) qui est habituellement un habitat avec des fluctuations thermiques de grande amplitude. Durant la période 2012-2016, mes efforts se sont portés principalement sur ces 2 habitats. Récemment, j'ai initié des recherches sur un milieu bien plus homogène : le milieu aquatique lentique (mares, étangs ; **section 1.5**) et son influence sur l'écologie thermique des larves de macro-invertébré aquatiques. Également, je commence à aborder un milieu bien plus spécifique que ceux évoqués jusqu'ici : le microclimat généré par les fleurs thermogéniques (**section 1.5**) qui doit être proche de celui des feuilles des plantes, mais qui n'est utilisé que ponctuellement par les organismes symbiotiques (pollinisateurs). Enfin, je termine ce rapport d'activité sur l'apport de ces recherches sur les questions sociétales qui importent pour l'INEE (**section 1.6**) : les impacts du changement global sur la biodiversité et la biologie de la conservation.

## 1.2 Conceptualisation de l'importance du microclimat

### ► *Perspectives conceptuelles en écologie du changement (micro)climatique*

L'approche la plus utilisée actuellement pour détecter et analyser les impacts du changement climatique sur la répartition géographique des organismes consiste à modéliser la distribution des espèces sur la base de la relation contemporaine entre climat et présence ('*species distribution models*', SDMs). Ces modèles intègrent des données climatologiques acquises à des échelles spatiales assez larges. Par exemple, la première base de données utilisée par les chercheurs dans le monde, WorldClim, renvoie des données pour des mailles géographiques de 1 à 10 km de côté. En collaboration avec Prof. Arthur Woods et sa postdoc Kristen Potter, nous avons effectué une analyse approfondie de la littérature pour quantifier cette différence entre l'échelle spatiale à laquelle les données climatiques sont récupérées et la taille corporelle des organismes étudiés. Ainsi, l'échelle spatiale des données climatologiques est 1 000 à 10 000 fois supérieure à la taille corporelle des plantes et des animaux, respectivement (Fig. 2). L'utilisation de telles données climatiques gomme donc totalement l'hétérogénéité climatique mesurable à des échelles fines. Une question primordiale est de comprendre à quel point cette hétérogénéité est importante pour les organismes, en leur permettant notamment de se maintenir dans des zones jugées défavorables d'un point de vu global.

Notre analyse dénonce non seulement un problème d'échelle spatiale, mais aussi un problème d'échantillonnage de la biodiversité. En effet, les études se concentrent principalement sur des organismes de taille moyenne à grande, mais le pic de taille corporelle de la biodiversité animale et végétale se situe bien en dessous de cette zone. En d'autres termes, notre évaluation ne concerne qu'une infime partie de la biodiversité, et surtout elle ignore la façon dont les plus petits organismes peuvent répondre aux changements environnementaux. Aussi, nous échantillonnons les données climatiques à des échelles qui ne correspondent à aucune taille corporelle dans ce contexte d'études sur la distribution géographique des organismes. Mes résultats de recherche que je détaille plus bas montrent pourtant que l'environnement peut être décrit à petite échelle et surtout que les petits organismes vivent dans des microhabitats hétérogènes à très petite échelle.



**Figure A1.2.** Longueur des cellules climatiques (Grid length) dans plus de 200 études modélisant les aires de distributions d'espèces (SDMs), comparée à la taille des animaux ou des plantes en question (Organism length). Les points colorés indiquent les tailles corporelles issues de chaque étude. Les lignes horizontales colorées montrent les intervalles de taille corporelle lorsque l'étude traitait de plusieurs espèces. Les points et lignes grises correspondantes indiquent la taille des cellules climatiques utilisées dans ces études. Le graph en dessous montre les distributions (échelle log) du nombre d'espèces étudiées pour chaque échelle spatiale. La distribution de May montre la distribution des tailles corporelles dans le règne animal. Voir article correspondant dans *Global Change Biology* (2013).

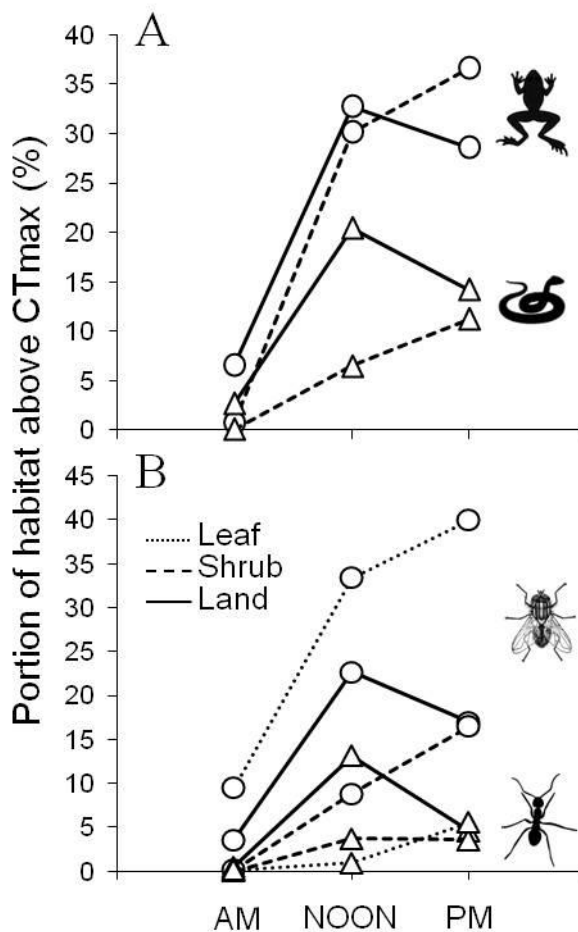
► **Un problème d'échelle spatiale : quelle hétérogénéité prendre en compte ?**

L'analyse évoquée précédemment (*Global Change Biology* 2013) ne fait qu'effleurer ce problème d'échelle spatiale dans le contexte relativement restreint de l'impact des changements climatiques sur la distribution géographique des espèces. Se pose la question de manière plus générale de quelle hétérogénéité climatique doit-on considérer dans ce concept de microclimat comme modérateur des effets des changements climatiques. Je suis donc allé plus loin en prenant 2 axes différents et

complémentaires pour quantifier l'hétérogénéité thermique à différentes échelles spatiales : en suivant un axe expérimental, en mesurant directement cette hétérogénéité thermique dans un paysage, puis un axe généraliste, en agglomérant des données publiées d'hétérogénéité thermique à plusieurs échelles.

*Axe expérimental* — La plupart des ectothermes tropicaux vivent déjà proches de leur seuil de tolérance à la température, du moins c'est ce qui est communément admis. Des effets importants du changement climatique sont donc attendus sous les tropiques malgré la faible amplitude du réchauffement. Toutefois, cette prédiction se base sur l'hypothèse que les ectothermes tropicaux vivent à la température de l'air telle que mesurée par nos stations météorologiques ou bien prédites par nos modèles globaux de circulation océanique. La température corporelle peut dévier de la température de l'air de façon substantielle lorsque ces organismes échantillonnent les microclimats à petite échelle. L'hétérogénéité thermique des paysages tropicaux a été rarement quantifiée en comparaison des paysages tempérés, ce qui nous empêche d'évaluer la vulnérabilité des ectothermes au réchauffement. J'ai ainsi quantifié l'hétérogénéité des températures de surface à différentes échelles spatiales, depuis l'échelle micro (une feuille d'arbre) jusque l'échelle du paysage (~50m) au sommet d'un Inselberg en Guyane française en utilisant une caméra thermique. Les Inselbergs sont souvent considérés comme des milieux extrêmes. Les données ont été collectées sur place en 2010 lors d'une mission entomologique financée par la Société Entomologique Antilles-Guyane et commandée par l'ONF. J'ai mesuré l'hétérogénéité des températures de surface à l'échelle de feuilles individuelles du buisson *Clusia*, en catégorisant les feuilles de soleil et d'ombre pour estimer l'hétérogénéité disponible pour des insectes phytophages par exemple, puis à l'échelle du buisson individuel de *Clusia* et enfin à l'échelle du paysage (plusieurs buissons et plusieurs espèces végétales) pour des ectothermes plus grands du type reptiles et amphibiens. La variance thermique variait d'une échelle à une autre, en augmentant vers l'échelle la plus grande. Plus surprenant, la variance thermique évoluait durant la journée mais de façon différente en fonction de l'échelle spatiale considérée : en augmentant graduellement au cours de la journée dans le cas de l'échelle d'un buisson mais en montrant un pic à midi dans l'échelle du paysage, par exemple. En comparant un jeu de données publiées sur les CTmax des ectothermes tropicaux (seuils critiques à la température) avec ces distributions de température de surface, j'ai pu montrer que la portion de l'habitat ayant des températures de surface supérieures au CTmax variait selon l'échelle spatiale et le taxon (Fig. 3). Ainsi les insectes sont plus particulièrement exposés au risque thermique à la surface des feuilles en plein soleil. Au contraire, les fourmis tolèrent les températures de surface élevées et peuvent survivre quasiment partout dans l'espace. De façon générale, et dans la limite de l'étude, il y a toujours au moins la moitié de l'espace qui correspond à des microclimats non létaux. Cette étude montre que la mosaïque de microclimat à fine échelle sous les tropiques module la vulnérabilité des ectothermes au réchauffement. En se déplaçant de quelques mètres, et même de quelques centimètres, les petits ectothermes tropicaux peuvent

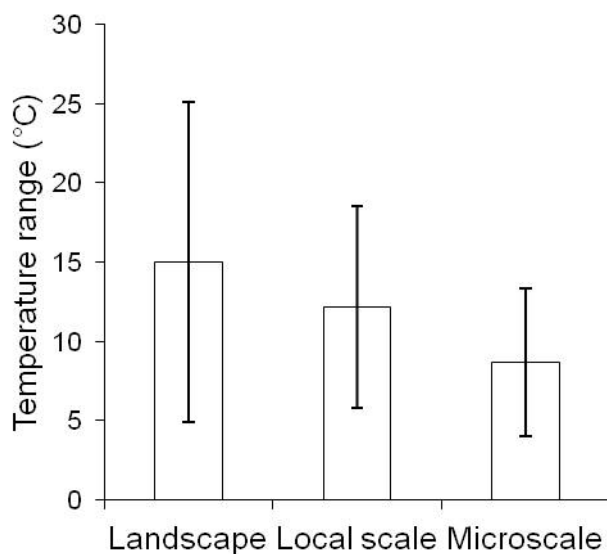
radicalement changer leur température microclimatique et donc échapper à la surchauffe.



**Figure A1.3.** Estimation de la vulnérabilité des ectothermes subtropicaux au réchauffement, en se basant sur la proportion de la distribution des températures de surface de l'habitat qui tombe au-dessus du CTmax des organismes pour les températures du matin (AM), du midi (NOON) et de l'après-midi (PM). (A) Pour les amphibiens (cercles) et les reptiles (triangles) à l'échelle du buisson (lignes en tirets) et du paysage (lignes pleines). (B) Pour les insectes (cercles) et les fourmis (triangles) sur des feuilles en plein soleil (lignes pointillées), à l'échelle du buisson (lignes en tirets), et à l'échelle du paysage (lignes pleines). Voir article correspondant dans *Integrative and Comparative Biology* (2016a).

**Axe général** — L'hétérogénéité climatique d'un paysage, combinée à la possibilité pour un organisme d'échantillonner cette matrice hétérogène, détermine le microclimat réellement vécu par l'organisme. Ces 10 dernières années, le nombre d'études rapportant des patrons microclimatiques à différentes échelles spatiales a considérablement augmenté. Lors du symposium "Beyond the Mean: Biological Impacts of Changing Patterns of Temperature Variation" organisé en marge de la conférence annuelle de la Society for Experimental Biology, j'ai mené un groupe de travail constitué de chercheurs internationaux (voir auteurs de l'article en question)

afin d'analyser cette littérature. Le but était de comparer les niveaux d'hétérogénéité thermique entre chaque échelle spatiale de façon générale. Nous avons également discuté des causes et conséquences de ces hétérogénéités pour la performance des organismes ectothermes. L'hétérogénéité thermique aux échelles locales et micro est principalement générée par l'architecture ou les caractéristiques géométriques des microhabitats. Malgré la difficulté à compiler des études qui diffèrent nettement dans leur design expérimental et leurs objectifs, notre étude montre que l'hétérogénéité thermique reste assez similaire aux différentes échelles spatiales depuis le micro jusqu'au paysage, et que l'intervalle de températures disponibles reste large ( $> 9^{\circ}\text{C}$ ; Fig. 4). Cet intervalle surpasse les amplitudes de réchauffement prédites sur le long terme pour les régions tropicales et tempérées. L'amplitude du changement thermique peut toutefois varier d'une échelle spatiale à une autre due aux interactions non-linéaires dans les budgets énergétiques des éléments d'un paysage. L'amplitude du réchauffement induit par le changement global peut être substantielle à l'échelle micro et moindre aux échelles locales et du paysage. Cette étude suggère que la mosaïque de microclimats est un modulateur primordial de la réponse de la performance des organismes et des interactions biotiques au réchauffement climatique.



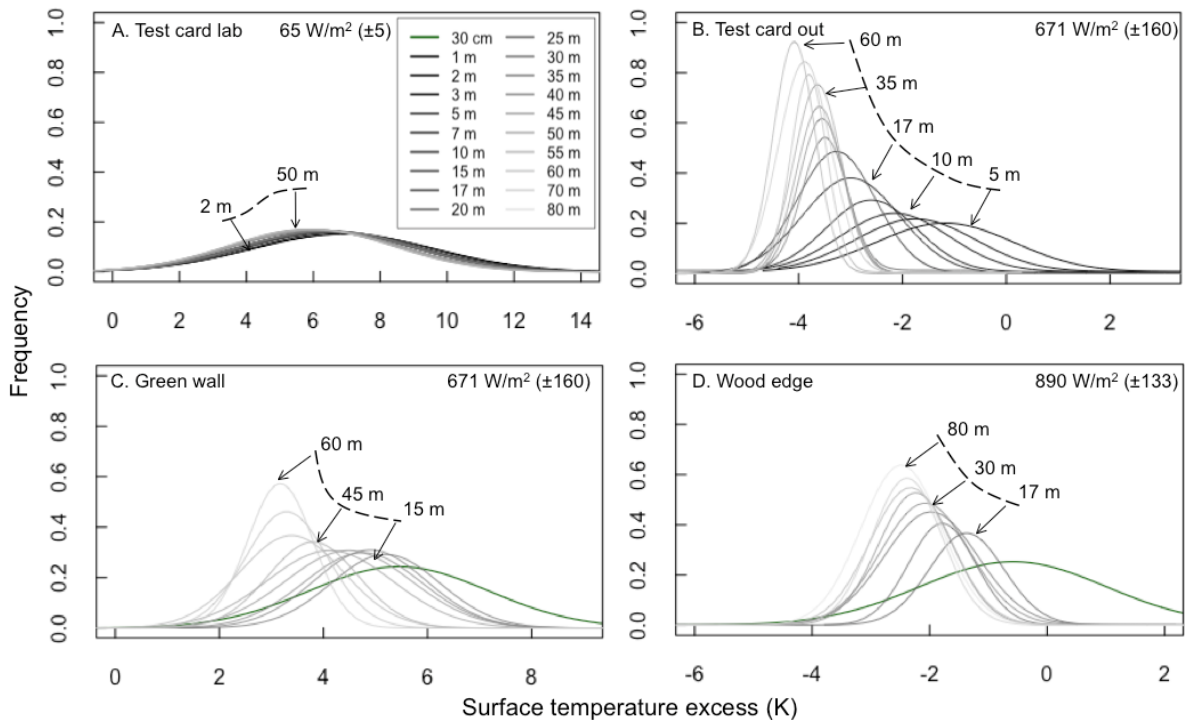
**Figure A1.4.** Intervalle de température moyen ( $\pm SD$ ) à trois échelles spatiales différentes. Le nombre d'études compilées : 3, 11 et 12 à l'échelle du paysage, locale et micro. Voir article correspondant dans *Integrative and Comparative Biology* (2016).



► *Caractérisation de la diversité microclimatique*

Ce lien entre échelle spatiale et variabilité microclimatique pose la question de comment mesurer et évaluer la diversité microclimatique disponible pour les organismes. Il n'est évidemment pas envisageable de scanner le moindre cm<sup>2</sup> de surface de notre planète avec une caméra thermique. En revanche nous pouvons améliorer nos connaissances sur les mécanismes des interactions entre le macroclimat et les objets vivants et inertes de l'environnement. Ces objets, de par leurs propriétés thermiques, produisent des mosaïques de température microclimatiques que les organismes peuvent utiliser. En collaboration avec les Prof. Arthur Woods (Univ Montana) et Michael Dillon (Univ Wyoming), nous avons tenté de catégoriser les différents microclimats suivant plusieurs axes (*Journal of Thermal Biology* 2015). Les microclimats abiotiques, générés par des éléments inertes (rochers etc.), sont bien plus prévisibles que les microclimats biotiques dont la température est générée par d'autres organismes, typiquement les plantes, et dont les réponses à l'environnement sont autrement plus complexes. Un autre axe de classification est l'effet du microhabitat sur la température atmosphérique. Certains microhabitats atténuent les amplitudes de variations de la température atmosphérique (ex: la température de l'eau dans un étang) quand d'autres amplifient les variations de température (ex: la température d'une feuille d'arbre au soleil). Egalement, un même type de microhabitat peut avoir un comportement différent (*buffer* ou *amplifier*) selon la latitude ou l'environnement. Notre synthèse de la littérature révèle enfin qu'il n'y a aucune théorie (et encore moins d'empirisme) sur comment les mosaïques microclimatiques évoluent avec la latitude et la biogéographie de façon plus générale, mais aussi sur comment la diversité microclimatique totale s'étalonne en fonction de la dimension du microhabitat. Ce domaine de recherche reste ouvert. Dans cette même étude (Woods et al. 2015), nous avons également considéré comment les ectothermes filtrent ces mosaïques microclimatiques en se déplaçant. Nous avons construit un modèle simple basé sur des règles de diffusion afin de simuler la façon dont un ectotherme peut échantillonner ces mosaïques microclimatiques en fonction de ses propriétés écophysiologicals (température optimale, CTmax etc.). Nous avons en particulier analysé l'effet d'un changement de la moyenne et de la variance des températures sur le comportement de thermorégulation. De façon générale, nos résultats montrent que des règles comportementales simples, et l'interaction entre la taille corporelle et le patron spatial des variations thermiques, influencent directement la distribution de la température corporelle au sein d'un paysage thermique. **Cette étude publiée dans un journal modeste (*Journal of Thermal Biology*, IF 1.5) a néanmoins été vue par toute la communauté de chercheurs travaillant sur les mécanismes de l'impact du changement climatique sur les ectothermes. Cet article a généré un grand nombre de citations, il était indiqué comme 'hot paper' dans le Web of Knowledge en 2016. Il est aussi parmi les articles les plus téléchargés sur le site du journal.**

La thermographie apparaît comme un outil incontournable, et de plus en plus abordable, pour mesurer les mosaïques thermiques à toutes les échelles spatiales. Toutefois, le biais potentiel dans la mesure de température de surface, causé par la distance entre l'objectif et la caméra thermique restait non quantifié. Les capteurs thermiques d'une caméra ayant une surface fixe, la taille du pixel d'une image thermique augmente avec la distance. Les constructeurs ne proposant pas de moyens d'évaluer le comportement de la température mesurée lorsque la caméra s'éloigne de la cible, nous avons élaboré un protocole de mesure de cet effet de la distance. Cette étude a été faite en collaboration avec un doctorant (Emile Faye) d'Olivier Dangles (DR IRD, Equateur). J'ai pu encadrer ce doctorant sur cette partie qui a ensuite été intégrée à sa thèse. Nous avons examiné l'effet de la distance entre 0,3 et 80 m sur différents métriques thermiques (moyenne, SD, *patch richness*, agrégation etc) et dans différentes conditions météorologiques pour différentes surfaces ayant une complexité structurale croissante (mire au laboratoire, mur végétalisé sur un château de la Loire, lisière de forêt). Nous avons trouvé que la distance est un modificateur de la température de surface mesurée par la caméra thermique (Fig. 5). Une relation non-linéaire existe entre la distance et la plupart des métriques thermiques avec une baisse rapide des métriques dans les 20 premiers mètres de distance puis une stabilisation au-delà de 20m. L'intensité des radiations solaires intensifie ce biais. Les températures de surface sont donc sous-estimées, en valeur absolue, et les mosaïques thermiques tendent à s'homogénéiser avec la distance avec un biais plus fort dans les parties les plus chaudes des scènes que dans les parties froides. Nous expliquons ce biais par l'influence de la composition atmosphérique qui augmente avec la distance et aussi par l'effet de la taille de pixel qui change avec la distance. Cet artéfact doit être considéré lorsque l'on souhaite comparer les mosaïques thermiques entre différentes échelles spatiales. **Cette étude publiée dans *Journal of Thermal Biology* représente une évaluation de la technique de mesure des mosaïques thermiques.**



**Figure A1.5.** Distributions de la fréquence des températures de surface obtenues à partir des images thermiques prises en se focalisant sur une mire (grille de carrés noirs et blancs) au laboratoire (A) et sur un mur végétalisé (B), et de toute la surface du mur végétalisé (C) et de la lisière de forêt (D) dans des conditions de ciel dégagé. Les courbes en vert représentent les distributions de température des feuilles des plantes (i.e. températures réelles). Voir Faye, Pincebourde and Dangles, *Journal of Thermal Biology* 2016 pour plus d'informations.

### ► Organisation du workshop international HETEROCLIM

*Workshop international HETEROCLIM:* la réponse des organismes au changement climatique dans des environnements hétérogènes. 10-14 Juin 2014, Loches, France.

*Organisateur principal:* Sylvain Pincebourde.

*Comité scientifique:* Sylvain Pincebourde, Olivier Dangles (IRD, Equateur), Jérôme Casas (IRBI) & Brian Helmuth (Northeastern Univ, USA).

*Participants:* 21 conférenciers invités (dont 14 étrangers) et 32 participants (dont 16 étrangers). <http://casas-lab.irbi.univ-tours.fr/heteroclim.html>

*Financements:* ANR, IRD, INEE, Conseil Régional Centre, Université François Rabelais.



Les chercheurs ont développé des méthodes sophistiquées pour prédire les impacts écologiques des changements climatiques. Toutefois, ces méthodes sont confrontées à une problématique d'échelle spatiale : les modèles climatiques prédisent la température pour des unités spatiales de 1 km<sup>2</sup> au mieux, ce qui est largement supérieur à la taille corporelle des organismes. Ces méthodes négligent

donc l'hétérogénéité climatique au sein des petites échelles. Pourtant, les dernières avancées montrent que, en théorie, les organismes tels que des insectes et des reptiles peuvent gommer une partie du réchauffement global en se déplaçant localement. Cependant, la recherche balbutie encore aujourd'hui sur la façon dont va répondre cette hétérogénéité spatiale au changement global.

L'objectif majeur du Workshop HETEROCLIM a été d'établir, pour la première fois, un état de l'art sur les processus liant l'hétérogénéité climatique aux différentes échelles spatiales avec la réponse des organismes. Le workshop a abordé des questions telles que comment un réchauffement global de quelques degrés va se répercuter au sein du microhabitat d'un organisme aussi petit qu'un insecte ou une plante. Aussi, l'ambition de ce Workshop a été de réunir les meilleurs chercheurs dans ce domaine afin d'initier de nouvelles collaborations spécifiquement dirigées pour avancer dans cette thématique. Ce projet nécessite d'incorporer des connaissances venant de disciplines très différentes : sciences de l'atmosphère, biogéographie, biologie thermique, écophysiologie animale et végétale, écologie biophysique, modélisation et statistiques. Ainsi, le workshop s'est décomposé en 3 sessions 'thématiques' : (i) comment connecter le changement global et le changement local voir microclimatique ? (ii) comment prédire la performance des organismes dans des environnements fluctuants ? et (iii) comment modéliser la distribution des organismes dans l'espace dans un climat changeant ? Une 4ème session a été dédiée au développement des stratégies de recherche pour les prochaines années (synthèse et perspectives).

Ce Workshop a initié la mise en place d'un réseau de recherche sur une thématique nouvelle en biologie du changement climatique. Cette thématique explose, et ce workshop réunissant les acteurs internationaux majeurs a permis de positionner la France, et en particulier le CNRS, l'IRD et l'Université François Rabelais, au centre de ce développement. Ce nouveau réseau a été au cœur d'un dépôt de projet au CESAB (FRB) en 2014 et 2015, mais sans succès. Une réflexion est en cours pour adapter ce projet et le soumettre à un appel H2020 courant 2020, projet dont je serais le principal coordinateur.

### *1.3 Le microclimat foliaire*

Le cadrage conceptuel décrit dans la section précédente résume le contexte dans lequel s'inscrivent mes études sur le microclimat foliaire. Une importante diversité d'organismes vit à la surface des plantes. Le microhabitat généré par les feuilles a donc un rôle écologique important. La surface d'une feuille est chauffée par le soleil, et refroidie par le vent et l'évapotranspiration, si bien que la température foliaire peut différer de la température ambiante de plusieurs degrés. Une question aujourd'hui encore non résolue, est comment le changement climatique à grande

échelle spatiale et temporelle va être transmise dans les espaces microclimatiques utilisés par les organismes à la surface foliaire ? En collaboration avec le Prof. Arthur Woods (en sabbatique au labo pendant 1 an), nous avons établi que l'état actuel de nos connaissances sur le fonctionnement du microclimat foliaire apporte une grande incertitude sur les prédictions du changement microclimatique à la surface des feuilles. Premièrement, il est nécessaire de mieux comprendre comment les stomates répondent aux fluctuations environnementales et aux dommages causés localement par les organismes phytophages. Ensuite, une étude récente a identifié un patron de température de feuilles d'arbres caractéristique à une échelle globale : bien que la température ambiante augmente depuis les régions boréales aux latitudes subtropicales, la température moyenne des feuilles d'arbres est remarquablement constante globalement. Aussi, à haute latitude, les feuilles sont plus chaudes que l'air ambiant, mais en sont assez proches à basse latitude.

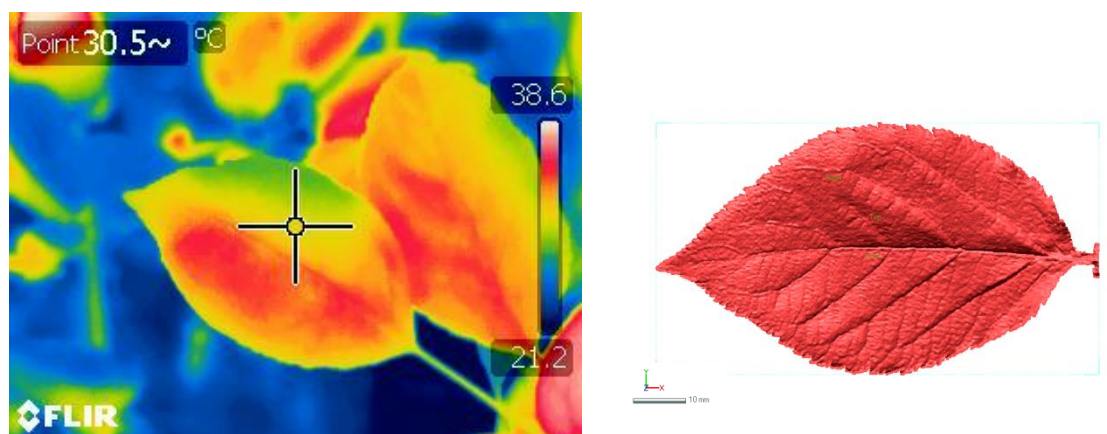
J'ai développé deux hypothèses conceptuelles afin d'anticiper la conséquence du réchauffement global sur ce gradient latitudinal (Pincebourde & Woods, 2012, *Functional Ecology*). La première hypothèse se focalise sur la capacité relative des feuilles subtropicales versus tempérées/boréales à 'gommer' les pics de température. En particulier, les feuilles subtropicales continueront à gommer les hausses de température faibles. Les organismes ne vont donc pas ressentir le réchauffement global annoncé alors qu'à haute latitude, les organismes vont subir ce réchauffement car les feuilles ne sont pas adaptées pour 'gommer' les températures élevées. La seconde hypothèse considère le degré d'adaptation des plantes aux conditions fluctuantes le long du gradient latitudinal. Plus spécifiquement, les feuilles à hautes latitudes seront pré-adaptées pour des températures encore plus élevées car ces plantes ont une histoire évolutive plus forte en relation avec les larges fluctuations journalières et saisonnières des conditions macro-climatiques. Cette hypothèse prédit que le microclimat des feuilles subtropicales est le plus susceptible de changer de façon disproportionnée comparé aux feuilles des zones tempérées et boréales. Les effets sur les arthropodes vivant à la surface des feuilles seraient importants, en particulier dans les zones subtropicales où la plupart des organismes subissent déjà des températures proches de leur seuil de tolérance thermique. Aussi, les avancées récentes en écophysiologie végétale réduisent le niveau d'incertitude climatique à la surface des feuilles. Des zones d'ombres importantes subsistent néanmoins et nous empêchent encore d'anticiper ces patterns décrits par nos hypothèses de travail. Ce constat a motivé le sujet de thèse que j'ai codirigé (Robin Caillon, voir plus bas).

Les objectifs de mes recherches sur le microclimat foliaire consistaient (i) à décrire ce microclimat dans le contexte thermique, (ii) à évaluer la réponse des insectes aux fluctuations de température de surface, (iii) et à étudier la dynamique des températures de feuilles au travers des échelles spatiales. Enfin, j'ai commencé à aborder le problème en intégrant d'autres facteurs que la température (composition en O<sub>2</sub> et CO<sub>2</sub>). De façon générale, la question posée est : **les organismes ont-ils la possibilité de se déplacer au sein des échelles locales (surface de feuille ou au travers de la canopée) pour gommer tout ou partie d'un changement climatique soudain ou chronique ?**



► **Microclimat foliaire : échelle de la feuille**

Je m'intéresse à l'impact de l'hétérogénéité de température de surface d'une feuille sur la distribution des organismes sur cette surface. La température de la surface foliaire varie spatialement suite à trois phénomènes : le phénomène de bord (le vent refroidi principalement le bord d'attaque), le 'stomatal patchiness' (l'ouverture stomatique est hétérogène à la surface) et la microtopographie (l'énergie radiative incidente est hétérogène sur la surface). En combinant quatre approches différentes (caméra thermique infrarouge, mesure de température par thermocouple, mesure de conductance stomatique avec un analyseur infrarouge d'échanges gazeux, acquisition de la microtopographie avec un scanner 3D à haute résolution) en conditions contrôlées, j'ai démontré et quantifié le rôle joué par la microtopographie foliaire dans l'hétérogénéité de température de surface foliaire chez le pommier. Les simples variations fines de microtopographie peuvent induire des variations de plus de 10°C d'un pixel à un autre à la surface foliaire (Fig. 6). L'effet de bord joue aussi un rôle important, en atténuant sur une partie de la feuille cet effet microtopographique. Chez le pommier, nous n'avons pas pu mettre en évidence le phénomène de stomatal patchiness, soit parce qu'il n'existe pas (à confirmer), soit parce qu'il ne se déclenche que dans des conditions climatiques particulières (ex : conditions chaudes et très sèches). Toutefois, les mesures d'hétérogénéité de température de surface foliaire faites dans des conditions climatiques variables montrent que la surface foliaire tend à s'homogénéiser lorsque la température ambiante augmente. Cette homogénéisation thermique s'opère via l'abaissement de l'excès température des zones les plus chaudes de la feuille uniquement, grâce à un mécanisme de thermorégulation de la plante. Les stomates se referment lors de la période de stress thermique, mais le déficit de vapeur d'eau est tel que la diffusion passive par les stomates devient proportionnellement plus importante dans les zones les plus chaudes.



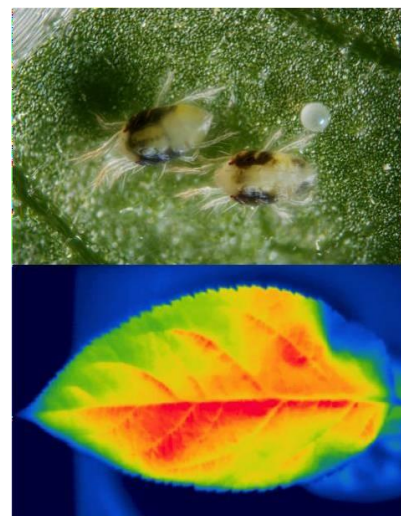
**Figure A1.6.** [A gauche] Image thermique infrarouge d'une feuille de pommier en plein soleil en verger. L'hétérogénéité de la température de surface est générée par la variation de l'angle d'incidence de la micro-surface due à la microtopographie : la zone la plus chaude de la feuille en rouge (33,5°C) correspond à la zone qui est à l'aplomb du rayonnement incident. La zone la plus froide en vert (26,3°C) correspond au bord de la feuille qui est refroidie par le vent. [A droite] Image

*d'une feuille scannée en 3D mesurant la microtopographie. Les zones sombres correspondent aux reliefs.*

Un modèle biophysique a été développé en collaboration avec Marc Saudreau (CR INRA, UMR PIAF, Clermont Ferrand) afin de modéliser cet effet de la microtopographie. Le modèle de spatialisation de la température foliaire prend en compte la géométrie de la feuille (microtopographie), les variables microclimatiques (température, humidité, rayonnement, vent) et le fonctionnement de la feuille (conductance stomatique, transpiration). Ce modèle couple un processus de triangulation de la feuille avec un bilan thermique de la surface foliaire. Une dynamique temporelle est intégrée via la dynamique des variables microclimatiques. Ce modèle a été validé après avoir mesuré expérimentalement des hétérogénéités de température de surfaces foliaires dans différentes conditions microclimatiques avec une caméra thermique. Des intervalles de températures importants ont été mis en évidence à la surface des feuilles de pommier : jusqu'à 20°C d'écart à la surface d'une seule et même feuille dans des conditions de radiations solaires élevées ! Notre travail montre que l'interaction entre les radiations solaires et la géométrie de la surface foliaire est le principal générateur de cette hétérogénéité. Cette étude représente l'analyse la plus complète jamais réalisée sur le budget thermique d'une feuille (publiée en 2017 dans *Plant Cell & Environment*). Ce modèle biophysique sera la première étape du couplage des échelles micro et globales. De tels écarts de température à l'échelle de quelques cm posent évidemment la question de comment aborder l'impact du changement climatique sur les organismes vivant à la surface des plantes.

### ► *La réponse des organismes au microclimat foliaire*

Les conséquences de cette hétérogénéité spatiale de la température de surface foliaire sur les organismes ont été étudiées. Des acariens jaunes (*Tetranychus urticae*) ont été filmés à la surface des feuilles, en parallèle d'un suivi en caméra thermique, dans des conditions contrôlées et pour différentes situations climatiques. En particulier j'ai analysé (avec l'aide d'un stage de M2) la distribution des acariens à la surface foliaire dans des conditions de température ambiante modérée (25°C) versus élevée (37°C), avec un niveau de radiations incidentes correspondant au plein soleil en été. Cette dernière condition rapproche les acariens de leur seuil de tolérance thermique que nous avons mesuré à 46°C. Comme précédemment, la température de surface foliaire est plus hétérogène à 25°C qu'à 37°C. Ainsi, à température modérée les acariens vivent dans un microclimat qui présente une gamme de température assez large. Un comportement de thermorégulation comportementale a été observé dans ce cas. Les



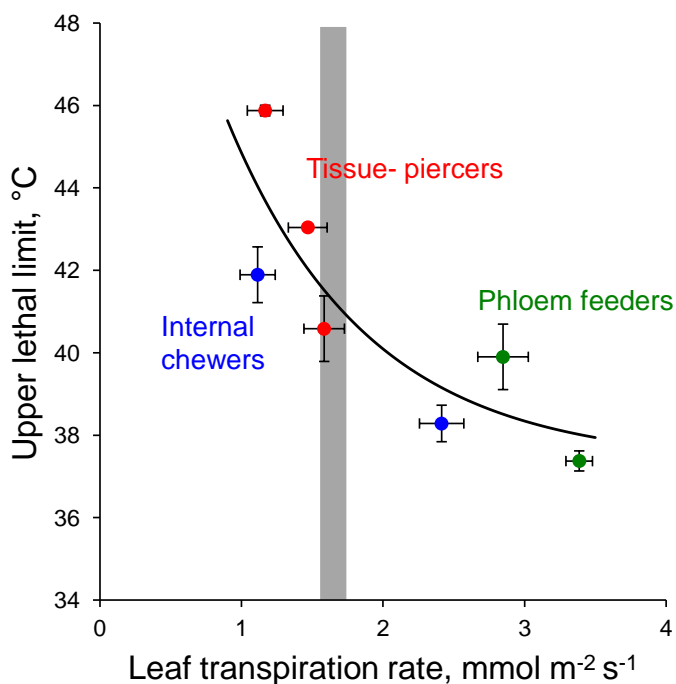


acariens tendent à se déplacer à la surface foliaire afin de trouver la zone foliaire qui les rapproche le plus de leur optimum pour leur développement (31°C). Au contraire, à température élevée, la surface est trop homogène thermiquement pour permettre un comportement d'évitement total des températures défavorables. Toutefois, même dans ce cas, un comportement d'évitement a été partiellement observé, leur permettant de s'éloigner du seuil léthal. Cette étude est la première à mesurer un comportement de thermorégulation d'un organisme dans la mosaïque de températures de surface foliaire. **Ces résultats exploratoires ont été publiés (Caillon et al. 2014, *Functional Ecology*) avec le stagiaire de M2 en 1er auteur, qui est devenu mon doctorant dans la foulée.**

Dans l'exemple des acariens ci-dessus, les mesures étaient réalisées avant que les acariens ne modifient fortement l'écophysiologie de la feuille. Nous avons aussi étudié le cas d'un insecte qui induit des modifications profondes dans le fonctionnement foliaire afin d'analyser le lien entre l'adaptation thermique de l'insecte et le niveau de modifications apportées à la feuille : le cas d'un insecte mineur de feuille. La chenille du microlépidoptère *Phyllonorycter blancardella* vit à l'intérieur de la feuille du pommier dans une structure appelée 'mine', qui correspond à une sorte de galerie. Les modifications apportées à la feuille sont de plus en plus importantes au fur et à mesure que la larve se développe, et elles sont de 2 types : changement dans la propriété de la surface de la mine à absorber les radiations dans le proche infrarouge, et modification de la courbe de réponse des stomates avec fermeture stomatique lorsque les radiations augmentent. Une approche de modélisation biophysique a été développée afin de prédire la température de la mine (microclimatique) en fonction de l'environnement et de ces modifications. En parallèle, les seuils de tolérance à la température ont été mesurés pour chaque stade larvaire. Cette étude montre clairement que le seuil léthal de température augmente au cours de l'ontogénie de l'insecte, de façon concomitante avec la température microclimatique. Une chenille âgée vit dans un microenvironnement plus chaud (réchauffement de 8°C par rapport au stade œuf) mais est plus tolérante aux fortes chaleurs (augmentation du seuil de 7°C par rapport au stade œuf). Ce résultat démontre le niveau d'adaptation thermique de chaque stade larvaire en lien avec les conditions microclimatiques. Nous avons également quantifié le biais dans les estimations de la tolérance au réchauffement climatique lorsque les conditions atmosphériques sont utilisées plutôt que les conditions microclimatiques. Le résultat est frappant : ignorer le microclimat cause un biais d'au moins 7°C (jusque 10°C suivant le stade larvaire) dans les estimations de la tolérance au réchauffement. L'intégration des conditions microclimatiques montre que malgré la variation des seuils létaux à la température durant l'ontogénie, les stades larvaires ont la même tolérance au réchauffement. **Cette étude a été publiée dans la revue *Ecology*, et elle constitue un point clé dans mes recherches car pour la première fois j'accède au degré d'adaptation de l'organisme aux conditions microclimatiques.**

L'insecte mineur de feuille est un cas particulier car l'insecte manipule son microenvironnement végétal. Toutefois, la plupart des ravageurs se nourrissent en étant à la surface de la feuille et en provoquant des dégâts variables mais sans pour

autant prendre contrôle de l'écophysiole de la plante que le fait la mineuse. C'est le cas par exemple des pucerons ou des acariens. Le lien entre l'adaptation thermique de ces arthropodes et les conséquences de leur nourrissage sur l'écophysiole de la plante a été analysé. Plus spécifiquement, les organismes qui provoquent une fermeture stomatique ou bien un assèchement des tissus foliaires induisent une augmentation de la température de surface foliaire. Ces organismes doivent donc montrer une plus forte résistance à la chaleur. A l'inverse, les insectes qui amènent une augmentation de l'évapotranspiration de la feuille vont aussi provoquer une baisse de la température de la surface foliaire, et devraient avoir une tolérance à la température plus basse. Nous avons testé cette hypothèse en combinant un modèle biophysique de température de surface foliaire et des mesures de seuil de tolérance à la température chez divers organismes (pucerons, acariens, mineuses, hémiptères). Le résultat montre une très nette relation non linéaire entre l'effet du ravageur sur le taux de transpiration de la feuille et son adaptation à la température, vérifiant notre hypothèse de départ (Fig. 8). Des changements microclimatiques à une échelle très fine, et particulièrement cryptiques, sont donc un moteur important de l'adaptation à la température. Nous montrons également que la méconnaissance de ces effets cryptiques des fluctuations microclimatiques cause des biais importants dans nos prédictions de la tolérance au réchauffement climatique dans cette communauté d'arthropodes. Ces mécanismes fins liant le microclimat et l'écologie thermique des ectothermes sont totalement ignorés dans les modèles macroécologiques contemporains qui tentent d'évaluer l'impact du changement global sur la biodiversité. Il reste donc encore beaucoup à faire afin d'incorporer cette démarche dans les modèles d'impact. **Cette étude constitue sans nul doute le point d'orgue du projet ANR Microclimite et de l'ensemble de mes études sur le microclimat foliaire. L'étude a été publiée dans la revue PNAS en 2019.**



**Figure A1.8.** Relation entre le taux de transpiration de la feuille du pommier durant l'attaque du ravageur et le seuil de tolérance à la chaleur du ravageur (moyennes  $\pm$  SD). La bande grisée indique le taux de transpiration de la feuille intacte sans ravageur. Chaque point représente une espèce. Ces espèces ont été catégorisées suivant leur mode de nourrissage : celles qui percent les cellules (rouge; ex: acariens), celles qui se nourrissent du phloème (vert; ex: pucerons) et enfin les espèces qui vivent dans le végétal (bleu; ex: mineuses).

### ► *Le microclimat foliaire au travers des échelles spatiales*

Cette section inclue en partie une thèse que j'ai codirigé (thèse soutenue en janvier 2016).

*Étudiant* : Robin Caillon (IRBI), bourse ministérielle.

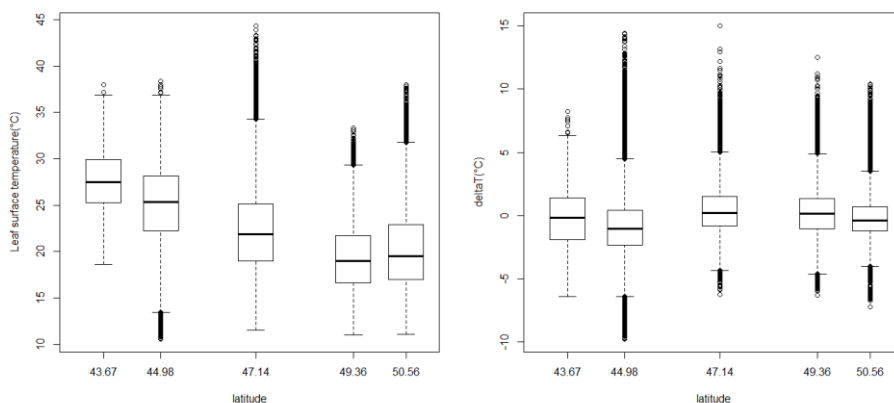
*Intitulé* : Biogéographie du microclimat foliaire : mécanismes et conséquences dans les relations plante-arthropode.

*Codirection* : Professeur Christelle Suppo (10%) et Dr. Sylvain Pincebourde (non HDR; 90%).

Il existe très peu de données quantitatives sur le profil du gradient latitudinal des conditions microclimatiques vécues par les organismes dans leur milieu naturel. Cette quantification est nécessaire pour évaluer l'impact réel du changement climatique sur la distribution géographique des organismes. De plus, le changement climatique prédit par le GIEC a une amplitude nettement différente en fonction de la latitude. Cette hétérogénéité géographique du changement climatique, couplée à la variabilité géographique potentielle du microclimat foliaire, rend difficile de prédire de façon intuitive l'amplitude du changement micro-climatique à venir. La thèse de Robin Caillon s'intégrait dans cette question importante, en mêlant expérimentation sur le terrain et en laboratoire, écologie des systèmes trophiques, éco-physiologie végétale et animale, et bioclimatologie. Sur la base de l'étude publiée par Helliker et

Richter (*Nature*, 2008), montrant que les températures de feuilles (plusieurs espèces d'arbres forestiers) tendent à converger vers 21°C des latitudes subtropicales aux latitudes boréales, nous prédisions une absence de gradient latitudinal des températures de feuilles du pommier, et des excès de chaleur des feuilles (différence avec la température ambiante) variables avec la latitude. Nous avons donc mesuré les températures de feuilles de pommiers à 5 sites le long d'un gradient géographique depuis la Belgique jusque Marseille pendant 2 années de croissance avec une résolution temporelle élevée (mesure automatisée toutes les 10 minutes). Nous avons également tenté de lier ce gradient latitudinal de température de feuille avec la résistance à la chaleur d'organismes vivant à la surface des feuilles (pucerons), et avec les processus d'adaptation de l'activité photosynthétique du pommier.

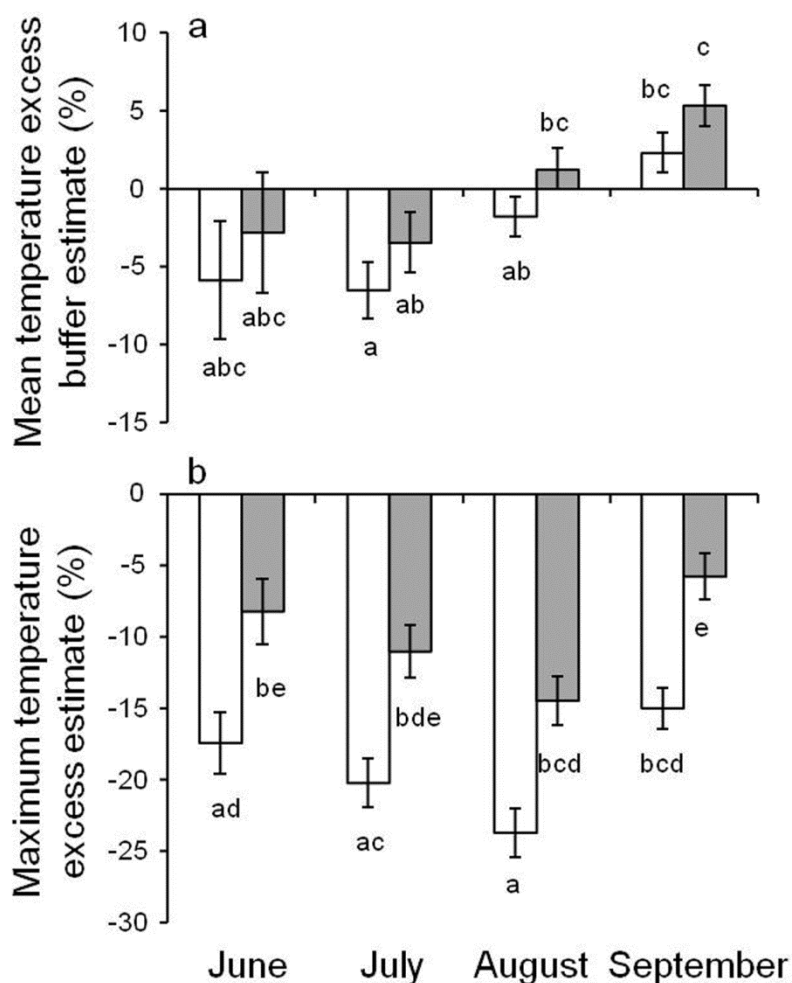
Contre toute attente, les résultats montrent un gradient marqué de température de feuilles de pommier suivant les variations géographiques de température de l'air (Fig. 9), ce qui vient réfuter notre hypothèse de départ. Toutefois, la variance thermique varie sensiblement avec la latitude. Ainsi, les organismes sur des feuilles aux petites latitudes subissent des variations thermiques de plus grande amplitude en comparaison d'organismes localisés sur des feuilles au nord.



**Figure A.1.9.** Box plot des températures foliaires (à gauche) et des excès de température foliaire par rapport à la température ambiante (à droite) pour la saison 2012 (mai à octobre) et les 5 sites d'étude. Les températures étaient échantillonnées toutes les 10 minutes dans la fenêtre 10h-16h.

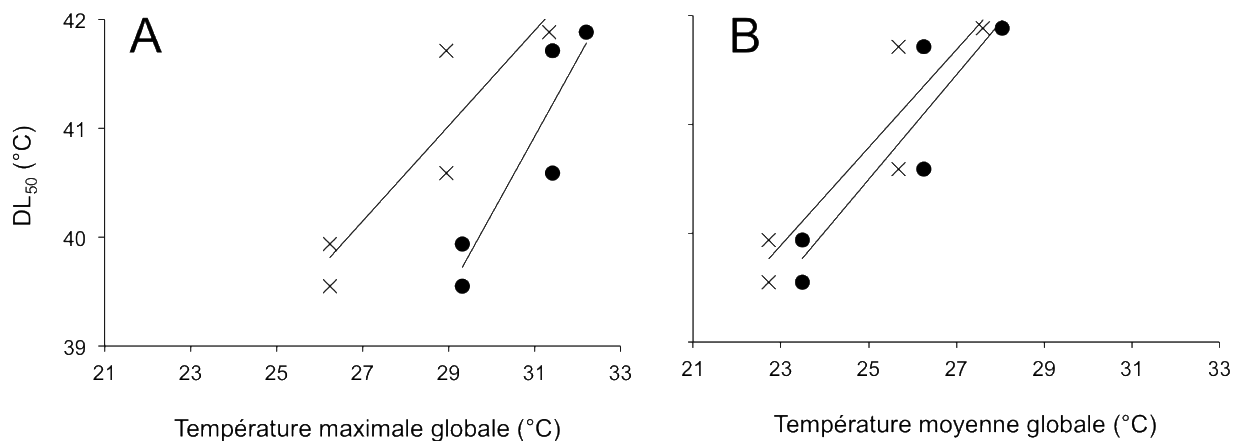
Dans le détail, ce travail de thèse a permis de quantifier la façon dont la plante 'gomme' les variations de température environnementale. La stratégie de thermorégulation des plantes consiste à diminuer l'excès de température des feuilles par rapport à l'air ambiant qui devient de plus en plus chaud. Cet aspect se lit dans la variation au cours de la saison de la capacité de la feuille à gommer une partie de l'amplitude de la hausse de température qui survient chaque jour (Fig. 10). Cette propriété se mesure à la fois pour la température moyenne journalière et pour la température maximale journalière. Par exemple (Fig. 10), en juin, lorsque la température moyenne journalière augmente de 1°C, l'excès de chaleur moyen des

feuilles par rapport à cet air ambiant diminue de 3-5% (i.e., 0.03-0.05 °C), tandis que l'excès de chaleur maximal (observé en général autour de midi) peut diminuer de presque 20% (i.e., 0.2°C) pour chaque augmentation de 1°C de la température de l'air. A l'inverse, en septembre, l'excès de chaleur moyen des feuilles tend à augmenter lorsque la température de l'air augmente (buffer positif) et l'excès de chaleur maximal journalier reste similaire à juin. Ces résultats montrent que la capacité des plantes à gommer des variations environnementales est importante, bien que non incluse encore à ce jour dans les modèles d'impact des changements globaux.



**Figure A.1.10.** Estimation de la capacité des feuilles à gommer l'amplitude des changements de température de l'air pour chaque période. Les estimations de cet effet 'buffer' sur l'excès de température des feuilles est montré pour l'excès de température moyen (a) et maximal (b) journaliers. La variabilité intra-canopée est montrée également en distinguant les feuilles situées à l'est (blanc) et à l'ouest (gris) du rang de pommier. Les données des 5 sites géographiques ont été agglomérées pour inférer la proportion de la variation de la température de l'air journalière qui est gommée par les feuilles. Un buffer de -10% signifie que l'excès de température de la feuille diminue de 0.1°C pour chaque augmentation de 1°C de la température de l'air (donc la feuille augmente de 0.9°C quand l'air se réchauffe de 1°C).

Nous avons identifié l'importance de ces effets 'buffer' à la fois pour la plante elle-même (activité de photosynthèse) et pour les ravageurs vivant à la surface des feuilles (pucerons verts). Le taux de photosynthèse a été mesuré sur les feuilles exposées au soleil sur chacun des 5 sites géographiques. Les pucerons ont également été échantillonnés sur les 3 sites situées les plus au sud du gradient. La température optimale pour la photosynthèse a pu être déterminée à partir des courbes de réponses à la température. Cette température optimale pour la photosynthèse varie le long du gradient latitudinal : elle est 10°C plus élevée près de Marseille qu'en Belgique. Pour chaque site, cet optimum photosynthétique est corrélé plus fortement à la température de feuille moyenne mesurée sur les 5 semaines avant la mesure de la photosynthèse qu'à la température maximale journalière. A l'inverse, la température létale des pucerons verts mesurée directement sur le terrain est plus fortement liée à la température de feuille maximale journalière de long du gradient (Fig. 11). En conclusion, différents métriques microclimatiques doivent être utilisés selon la performance ou l'organisme qui est étudiée.

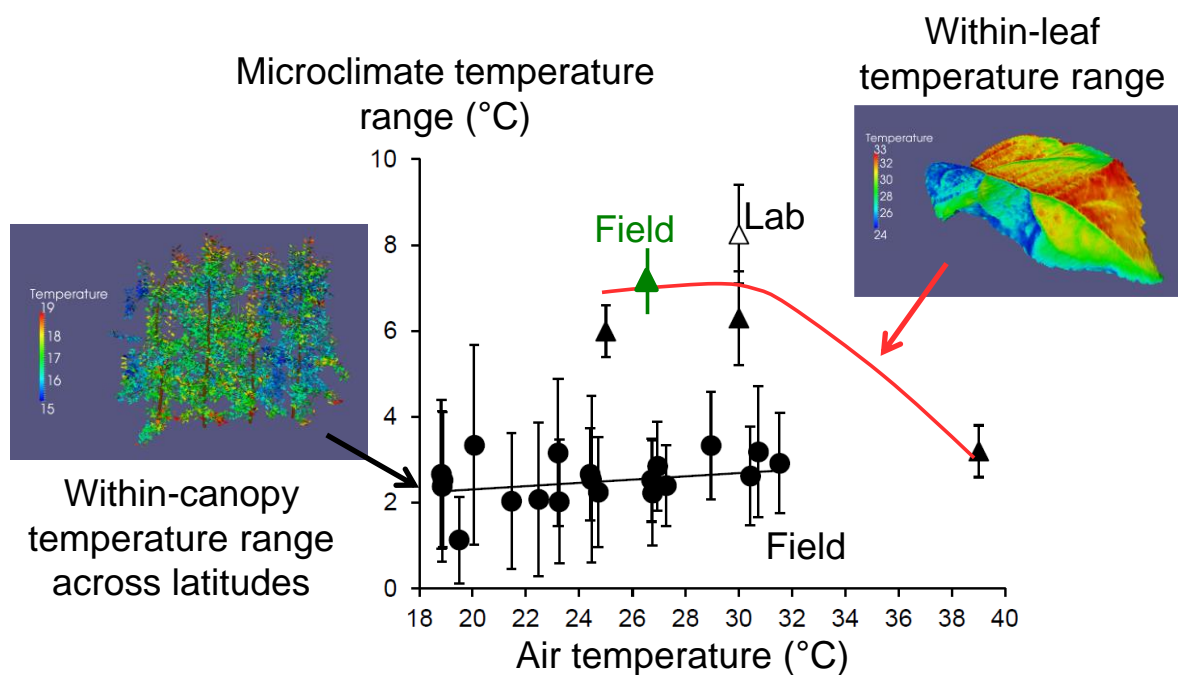


**Figure A.1.11.** Profil latitudinal de la DL<sub>50</sub> en fonction de la température maximale (A) et moyenne (B) globale de l'air (croix) et de la feuille (cercles). Les droites de régression sont indiquées en trait plein.

L'ensemble de ces données à l'échelle biogéographique a été combiné avec les données d'hétérogénéité de température foliaire à l'échelle de la feuille pour comparer l'hétérogénéité des températures de feuilles à différentes échelles spatiales. L'objectif est d'identifier l'échelle spatiale à laquelle l'hétérogénéité thermique est la plus importante. Les données à l'échelle de la feuille et des canopée le long du gradient latitudinal n'ont pas été mesurées avec les mêmes outils ni la même approche, mais cette comparaison permet d'évaluer l'influence du type de mesure sur l'estimation des niveaux d'hétérogénéité dans un contexte d'impacts des changements globaux. Cette comparaison montre que l'estimation de l'hétérogénéité thermique n'est pas la même suivant l'échelle spatiale considérée. Par exemple, l'intervalle des températures microclimatiques est plus élevé à l'échelle d'une surface foliaire (que ce soit sur le terrain ou en laboratoire) qu'à l'échelle d'une canopée (Fig. 12). Ce qui est

surprenant, c'est que l'intervalle de température à la surface d'une feuille individuelle est similaire à la variation de température de l'air le long d'un gradient latitudinal de 700 km. En d'autres termes, un acarien qui se déplace de quelques centimètres à la surface d'une feuille d'arbre peut subir la même variation de température qu'un acarien voyageant sur 700 km vers le nord. Ce résultat pose beaucoup de questions en termes de comment aborder la question de la prédiction de l'impact du changement climatique sur les organismes. Nos données permettent difficilement d'évaluer l'effet du réchauffement sur l'hétérogénéité thermique aux différentes échelles (Fig. 12), mais il semble que l'intervalle de température intra-feuille soit particulièrement sensible au réchauffement à partir d'un certain seuil, avec une homogénéisation thermique au-delà de ce seuil. Nous manquons encore de données pour vraiment statuer sur ce point.

**L'ensemble de cette section résume des résultats encore non valorisés en termes de publication (une publication est actuellement en révision pour la thèse de Robin Caillon). Une synthèse sur l'hétérogénéité thermique au sein des microclimats au travers des échelles spatiales et en fonction de la latitude est prévue dans un futur proche.**

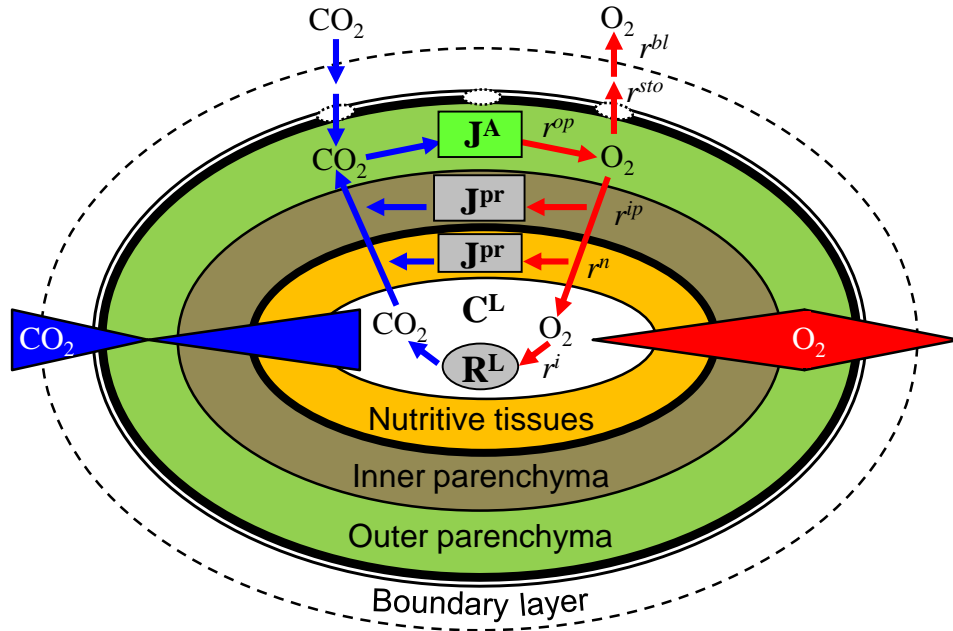


**Figure A.1.12.** Intervalle de températures microclimatiques en fonction de la température atmosphérique à l'échelle de la feuille de pommier (triangles) et à l'échelle des canopées le long du gradient latitudinal (cercles noirs). Des données acquises sur le terrain et en laboratoire ont été agglomérées.



## ► La dimension gazeuse du microclimat foliaire

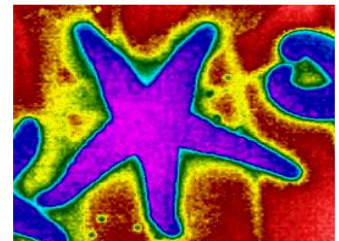
Mes études détaillées ci-dessus se focalisent principalement sur la température. Evidemment, le microclimat ne se résume pas seulement à ce facteur même si la température est probablement le facteur majeur due à ses effets sur les activités enzymatiques. La composition gazeuse est aussi une composante importante dans tout microenvironnement. La vaste majorité des organismes dépend des concentrations en O<sub>2</sub> et CO<sub>2</sub> dans l'air qu'ils respirent. Dans le cas des insectes vivant à l'intérieur des tissus des végétaux (mineuses, galles etc.), ces gaz sont échangés entre l'air ambiant et l'atmosphère à l'intérieur du microhabitat de l'insecte qui contribue à la modification de son microenvironnement en expirant du CO<sub>2</sub>. L'activité photosynthétique de la plante ainsi que la respiration des cellules du végétal participent également à modifier les concentrations en gaz au niveau de l'insecte. Toutefois, très peu d'études se sont portées sur le réseau d'échanges gazeux chez ces insectes endophages. Par une approche théorique et conceptuelle, j'ai identifié les mécanismes qui modulent la composition gazeuse au sein du microhabitat des insectes endophages. J'ai testé l'hypothèse que la simple position de la larve au sein des tissus de la plante peut être utilisée comme proxy du risque d'occurrence de conditions hypoxiques (pas assez d'O<sub>2</sub>) ou hypercarbiques (trop de CO<sub>2</sub>), malgré la grande diversité de traits d'histoire de vie de ces insectes. Un modèle de réseau de diffusion des gaz a été développé afin de déterminer la composition gazeuse dans le microhabitat des insectes (Fig. 13). Ce modèle a ensuite été appliqué aux insectes mineurs, aux galligènes et aux insectes creusant des galeries dans les plantes en intégrant les différents obstacles présents le long du trajet de la diffusion de l'O<sub>2</sub> et du CO<sub>2</sub>. La nature et la direction des transferts de gaz dépendent de la structure physique du microhabitat, de l'activité photosynthétique ainsi que du comportement des stomates dans les tissus de la plante. Nous avons identifié la position de l'insecte dans ce réseau de diffusion de gaz comme étant un facteur déterminant du risque d'exposition à l'hypoxie ou l'hypercarbie. Les différents types d'insectes endophages ont été rangés depuis le plus risqué ou moins risqué : mineuses du cambium > tunnels > grandes galles > petites galles > mineuses du bois > mines dans les plantes aquatiques > mineuses de feuilles. De plus, le CO<sub>2</sub> produit par les larves est certainement assimilé par les tissus de la plante durant la photosynthèse. La température microclimatique ainsi que la concentration atmosphérique en CO<sub>2</sub> modulent ces concentrations gazeuses. Nous prédisons que (i) l'hypoxie favorise indirectement l'évolution d'insectes galligènes tolérant au froid, et (ii) la normoxie dans les mines de feuille permet aux insectes mineurs de se développer à des températures élevées. L'endophagie contraint les processus de diffusion de gaz avec des conséquences sur l'écologie évolutive des insectes endophages. **Cette étude particulièrement lourde conceptuellement a été publiée dans un numéro spécial de la revue *Journal of Insect Physiology* (Pincebourde and Casas, 2016) sur les insectes re-programmeurs des plantes.**



**Figure A.1.13.** Vision schématique du réseau de diffusion de gaz dans une galle de cynipid contenant des stomates (coupe transversale). La zone en blanc au centre de la galle correspond à la chambre larvaire avec une concentration en gaz  $C^L$ . Le cercle gris montre la position de la larve et les zones vertes représentent les zones ayant une activité photosynthétique. L'épiderme de la galle est indiqué par la ligne située entre la limite de la couche mince et le parenchyme externe. Cet épiderme contient les stomates au travers desquels les échanges de gaz se déroulent. Les gradients de concentration en  $O_2$  et  $CO_2$  au travers de la galle sont indiqués en rouge et bleu, respectivement. Le réseau de résistance inclut la couche mince ( $r^{bl}$ ), les stomates ( $s^{to}$ ), le parenchyme externe ( $r^{op}$ ) et interne ( $r^{ip}$ ), de la couche nutritive ( $r^n$ ) et de la chambre larvaire ( $r^i$ ). Schéma non à l'échelle par souci de clarté.

### 1.4 Le microclimat en zone d'estran

Je poursuis le travail commencé durant mon séjour postdoctoral aux États-Unis en 2006-2007. Des nouvelles analyses et travaux de modélisation viennent alimenter aujourd'hui ces données. Bien que ce chapitre de mes recherches soit focalisé sur l'écosystème intertidal, les thématiques et questions écologiques abordées sont particulièrement pertinentes pour mes recherches sur les relations insecte- plante.

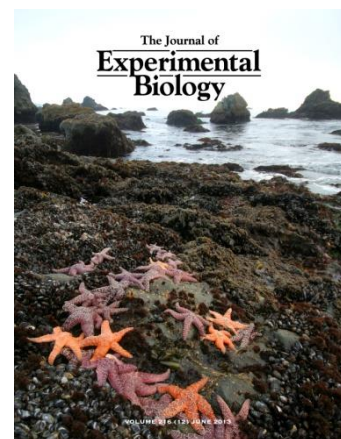


L'impact de la température sur les mécanismes physiologiques a été largement étudié chez de nombreux organismes. La température corporelle des organismes ectothermes agit comme un filtre à l'interface physiologie – environnement. Cependant, encore à ce jour, la température corporelle de la plupart

des organismes n'a pas été quantifiée dans les conditions naturelles. Cette absence de connaissance est un handicap majeur pour prédire l'influence de la température sur la distribution géographique des espèces et l'impact potentiel du climat passé, présent et futur sur la persistance des populations dans la nature. L'objectif de mon projet est de souligner l'importance de regarder la température corporelle des organismes lors d'études en écologie thermique, en révélant des mécanismes d'interaction organismeI-organismeII-environnement articulés autour des patrons de température corporelle. Le projet détermine l'impact des variations climatiques sur une relation proie – prédateur (moule californienne *Mytilus californianus* – étoile de mer *Pisaster ochraceus*) dont le rôle dans la gestion de la biodiversité est crucial au sein de l'écosystème intertidal ('*keystone species*'). Les organismes intertidaux subissent d'importants écarts de température (de l'ordre de 10 à 30°C quotidiennement) entre l'immersion à marée haute et l'émersion à marée basse. La répartition de *Mytilus* dans la zone intertidale est délimitée par l'action directe du stress physiologique (température), et par l'activité du prédateur *Pisaster*. Les mécanismes d'interactions thermiques entre le prédateur et son environnement abiotique sont détaillés, puis leurs effets sur l'intensité de la relation proie-prédateur sont quantifiés pour différents niveaux de complexité environnementale. Dans l'ensemble, la presse internationale a largement couvert ces études (research highlights dans les revues *Nature*, *Science*, puis *National Geographics*, BBC etc.).

### ► *Capacités de thermorégulation*

Les mécanismes de thermorégulation peuvent permettre à l'animal d'éviter des conditions stressantes parfois de façon cryptique, invisible à l'observateur humain. Le prédateur *Pisaster* thermorégule selon deux mécanismes distincts. Tout d'abord, la température de l'océan durant la période d'immersion précédant la marée basse influence la valeur maximale de la température corporelle durant la marée basse, due à une inertie thermique importante. Ainsi, lors des périodes d'eaux froides le prédateur peut échapper aux conditions aériennes stressantes. Ensuite, lorsque ce prédateur est exposé durant une marée basse à des hautes températures, il montre la capacité d'accumuler plus d'eau de mer dans ses cavités corporelles afin d'accroître d'avantage son inertie thermique, résultant en une baisse significative de sa température corporelle durant les marées basses suivantes. Cette étude révèle, pour la première fois chez un organisme ectotherme, une capacité thermorégulatrice impliquant l'ajustement de l'inertie thermique de l'animal. Toutefois, cette stratégie présente une faille puisque l'animal reste dangereusement exposé durant la première marée basse avec des températures corporelles élevées. Là encore, mes travaux révèlent une adaptation tout à fait singulière chez *Pisaster*. Cette étoile de mer ajuste son hétérogénéité thermique régionale : les 5 bras restent plus chauds que le corps central où se trouvent les



organes vitaux. L'échinoderme semble être capable de dériver la chaleur absorbée par le corps central vers les bras. Ceux-ci peuvent être détachés par autotomie dès lors que l'excès de chaleur provoque des lésions internes. Ceci permet à l'étoile de mer de survivre (malgré la perte d'un ou plusieurs bras) à une exposition thermique intense et de courte durée. L'ensemble de ces résultats montre que cette étoile de mer est un véritable *thermal warrior* au sens de Bernd Heinrich.

### ► *Impacts d'un environnement à stress multiples*

Les études expérimentales du réchauffement climatique testent en général les effets écologiques de traitements en conditions constantes, et négligent souvent l'influence des fluctuations environnementales pourtant plus réalistes. De plus, les organismes subissent de multiples événements stressants au cours de leur vie, et plusieurs stress peuvent interagir de façon non-additive, ce qui complexifie les influences environnementales sur les taux physiologiques et les traits d'histoire de vie. Toutefois, très peu d'études ont regardé comment les interactions temporelles entre différents épisodes de stress environnemental peuvent influencer les interactions biotiques. Ici, j'ai mesuré la réponse du taux de prédation à différents niveaux de coïncidence temporelle de différents événements de stress thermique chez cette étoile de mer (*Pisaster ochraceus*). Sur la base des séries temporelles de températures corporelles, nous avons mis au point des expériences en laboratoire visant à tester l'influence des variations des températures corporelles aquatiques et terrestres sur le taux de prédation, en conditions constantes et fluctuantes. Le design expérimental permettait de contrôler l'intensité (moyenne), la variance et le patron temporel des variations pour les deux facteurs (températures corporelles aquatiques et terrestres), ainsi que le degré de coïncidence temporelle entre périodes de température élevée à marée haute et à marée basse. L'expérience en conditions 'constantes' montre que le taux de prédation diminue lorsque la température corporelle terrestre augmente de 16°C à 27°C. À l'inverse, le taux de nourrissage est maximal à une température aquatique intermédiaire de 13°C dans l'intervalle 10°C-16°C. La norme de réaction du taux de nourrissage du prédateur a pu être modélisée en fonction des deux températures, c'est-à-dire sous forme d'une norme de réaction 3D, ce qui est unique. Cependant, cette norme de réaction ne permet pas de prédire de façon fiable le taux de prédation dans des conditions de fluctuations environnementales à cause des fortes interactions temporelles entre les deux températures. Le taux de prédation diminue fortement à mesure que la variance thermique augmente. Aussi, de façon surprenante, le taux de prédation diminue à mesure que les deux événements de stress thermiques (aquatiques et terrestres) ne coïncident plus dans le temps, malgré une moyenne et une variance de température similaires entre les traitements. Le taux de prédation est le plus élevé lorsque ces deux stress s'appliquent dans la même fenêtre temporelle. Connaître le timing précis des différents événements stressants les uns par rapport aux autres est essentiel pour prédire les réponses des organismes au changement global. **Cette étude publiée**

**dans *Ecology Letters* (Pincebourde et al. 2012) apporte un jeu de données rare dans le domaine de l'étude des effets de la moyenne, de la variance et des patrons temporels du stress. Cette étude m'a permis de développer une autre collaboration importante aujourd'hui avec Dr. Apostolos Koussoroplis (postdoc en Allemagne) qui a réutilisé ce jeu de données pour valider un modèle permettant d'intégrer les effets d'environnements multifactoriels et fluctuants sur la performance des ectothermes (Koussoroplis, Pincebourde and Wacker, *Ecological Monographs*, 2017).**

### *1.5 Autres microclimats particuliers*

Depuis quelques années, j'applique mon approche microclimatique à d'autres systèmes dans le but de compléter ma vision du lien entre la variabilité microclimatique et les adaptations thermiques des organismes. Ainsi, j'ai recherché un écosystème présentant à priori une variabilité microclimatique plus faible que les deux systèmes présentés ci-dessus (surface foliaire et zone d'estran). Mon choix s'est tourné rapidement vers l'écologie aquatique : les milieux aquatiques lenticules. La température de l'eau dans les zones humides est habituellement considérée comme moins fluctuante que la température atmosphérique. Comment cela se traduit-il en termes d'adaptations à la température des macroinvertébrés aquatiques ? Peut-on malgré tout observer un comportement de sélection de microclimats dans cet environnement aquatique à priori plus homogène ?

Depuis 2015, je m'intéresse également au cas des plantes thermogéniques. Les fleurs de ces plantes produisent de la chaleur dans un contexte de pollinisation le plus souvent, se traduisant par des températures de fleur élevées. Ces fleurs sont visitées par des insectes qui passent donc une petite partie de leur vie à ces températures élevées. Ce cas est un autre exemple intermédiaire de fluctuations microclimatiques survenant pendant une courte durée. Comment une exposition aussi courte à des températures élevées peut-elle influencer les adaptations thermiques de ces insectes ?

Enfin, l'ensemble des microclimats étudiés ci-dessus varient thermiquement principalement due à la source de chaleur dans l'environnement : les radiations solaires. La question de l'importance de ces microclimats peut donc être inversée pour rechercher en quelques sortes le témoin : que se passe-t-il la nuit en l'absence de radiations ? De nombreux insectes nocturnes pratiquent l'endothermie (production de chaleur métabolique) pour palier à l'absence de source de chaleur dans leur environnement. Quelles sont les conséquences d'une telle stratégie dans un contexte de changement climatique ? J'ai démarré des études sur ce sujet en 2015 avec un stage de M2.



► *Le microclimat en écologie aquatique*

*Collaboration* : Association naturaliste ANEPE Caudalis (Renaud Baeta et Eric Sansault).  
Obtention du **Trophée du Mécénat d'Entreprise (2014)** décerné par le Ministère de l'Ecologie, du développement durable et de l'énergie.



Le milieu aquatique, en particulier les eaux stagnantes, est considéré comme plus constant et stable que le milieu terrestre d'un point de vue thermique. Cette propriété est due notamment à la forte inertie thermique de l'eau en général. Cependant, la température de l'eau dans une mare ou un étang peut aussi montrer des fluctuations quotidiennes, qui se rajoutent aux fluctuations saisonnières. Ces dernières sont assez bien documentées dans la littérature. Beaucoup moins d'études se sont focalisées sur l'impact des fluctuations quotidiennes de température de l'eau sur la faune de macroinvertébrés. En particulier, certaines espèces telles que les Odonates se basent en partie sur la température de leur habitat pour initier la phase d'émergence (sortie de l'eau de la larve aquatique pour effectuer la dernière mue). Dans cette étude (projet Od'SPOT), mon objectif est de caractériser la dynamique temporelle de la température de l'eau dans l'habitat des larves d'Odonates sur plusieurs sites différents.

Les résultats montrent une variabilité spatiale et temporelle de la température de l'eau très importante. L'amplitude de la fluctuation quotidienne de la température varie d'un habitat à l'autre au sein de chaque site, allant de 1-2 °C seulement à plus de 10 °C. Cette différence est liée principalement à l'orientation des berges par rapport au soleil et au niveau de turbidité de l'eau. Les différences entre habitats sont également d'amplitude très variable, jusque 11°C de différence entre 2 habitats éloignés de seulement quelques mètres. La distribution des sites d'émergence des Odonates est également très hétérogène. Tandis que la température microclimatique vécue ne semble pas influencer sur le taux d'émergence, la plupart des espèces Odonates montrent une préférence pour certains habitats ayant un microclimat particulier. En été, lorsque les températures ambiantes sont élevées, les émergences se déroulent dans les microhabitats les plus frais. A l'inverse, au printemps, les pics d'émergence sont observés au sein des microhabitats montrant des fluctuations thermiques de plus grande amplitude. Dans un contexte de changement global, ces résultats génèrent beaucoup de questions sur les effets potentiels du réchauffement sur les phénologies d'Odonates. Ce travail réalisé avec le support d'un stage de M2 est en cours de valorisation.

Une autre partie du projet Od'SPOT consistait à évaluer la capacité de dispersion d'une espèce Odonates rare et menacée, emblématique de la Région Centre : la leucorrhine à large queue. Cette étude réalisée en collaboration étroite avec l'association naturaliste Caudalis se basait sur l'utilisation de la télémétrie pour suivre les adultes immatures après leur émergence afin de déterminer l'habitat de

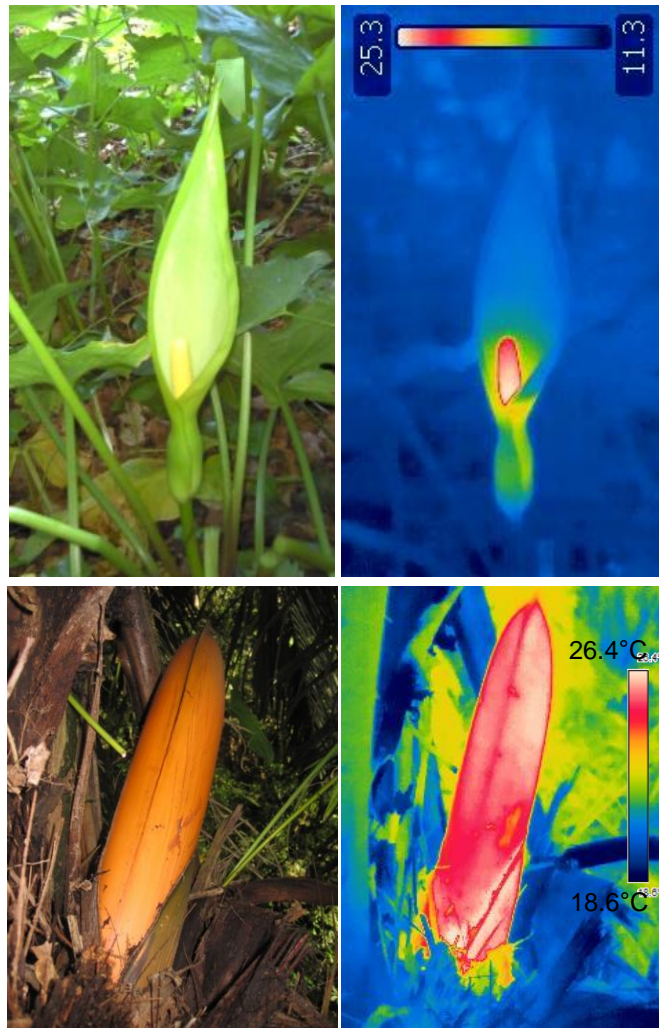
maturation et de quantifier leur capacité de dispersion. Le but était d'estimer la capacité de colonisation de sites éloignés à partir des quelques populations sources présentes dans la région. Malgré des difficultés techniques inhérentes à la méthode de télémétrie, les résultats suggèrent que l'espèce disperse assez peu. Plus important, les résultats démontrent que le microhabitat utilisé par les immatures pour murer sexuellement se situe dans la canopée des grands chênes situés autour des mares forestières (à environ 30m de haut). Du point de vue conservation de l'espèce, ce résultat apporte des informations cruciales.

Enfin, plus récemment, j'ai monté le projet régional PROTECTODO afin d'étudier l'écophysiole thermique des larves d'Odonates. En effet, l'écologie des stades adulte des libellules est bien couverte mais paradoxalement nos connaissances sur l'écologie des larves aquatiques sont très limitées. Le projet qui a démarré il y a 1 an et demi consiste à mesurer les effets de la température de l'eau, de la quantité de nourriture et de l'oxygène dissout dans l'eau sur la croissance des larves de plusieurs espèces dont la leucorrhine à large queue. Un laboratoire dédié à l'écologie aquatique expérimentale est en cours de montage à l'IRBI pour répondre aux besoins.

### ► *Le microclimat des fleurs thermogéniques*

La production de chaleur par les plantes (thermogénèse) est intéressante dans mon contexte microclimatique car ce phénomène génère une source de chaleur alternative au soleil pour certains insectes ou autres microorganismes. En collaboration avec Olivier Dangles (IRD) et Prof. Rommel Montufar (PUCE, Quito, Equateur), le spécialiste en Equateur des palmiers, nous avons étudié la thermogénèse chez le palmier Tagua (*Phytelephas aequatorialis*). Ce palmier à une importance économique et sociale élevée car il est utilisé dans plusieurs industries et activités locales. Ce palmier est dioïque, avec des arbres mâles et des arbres femelles. Les fleurs mâles et femelles sont très différentes, en particulier en taille (plus de 2m pour les inflorescences mâles et à peine 30 cm pour les femelles), et en durée de vie (1 jour pour les mâles contre 1 semaine pour les femelles). La production de chaleur par les fleurs mâles était connue sans n'avoir jamais été vraiment mesurée et décrite. Elle demeurait inconnue pour les fleurs femelles. En combinant l'utilisation d'une caméra thermique et de dataloggers miniaturisés, nous avons caractérisé avec précision la dynamique de la production de chaleur des 2 types de fleur. Le résultat le plus frappant est que la thermogénèse se déroule non pas durant le stade de fleur ouverte, mais durant le stade de bourgeon floral (Fig. 14). La fonction de cette thermogénèse particulière n'est pas encore élucidée, mais des pollinisateurs spécifiques ont été observés sur les bourgeons lors de la production de chaleur. Il semble aussi que ces bourgeons soient capables de thermoréguler assez finement puisque des températures assez semblables ont été mesurées dans différentes conditions de température ambiante. **La découverte a été publiée dans la revue phare *Frontiers in Ecology and the Environment*, et une autre publication avec les données quantitatives est en cours d'écriture.**





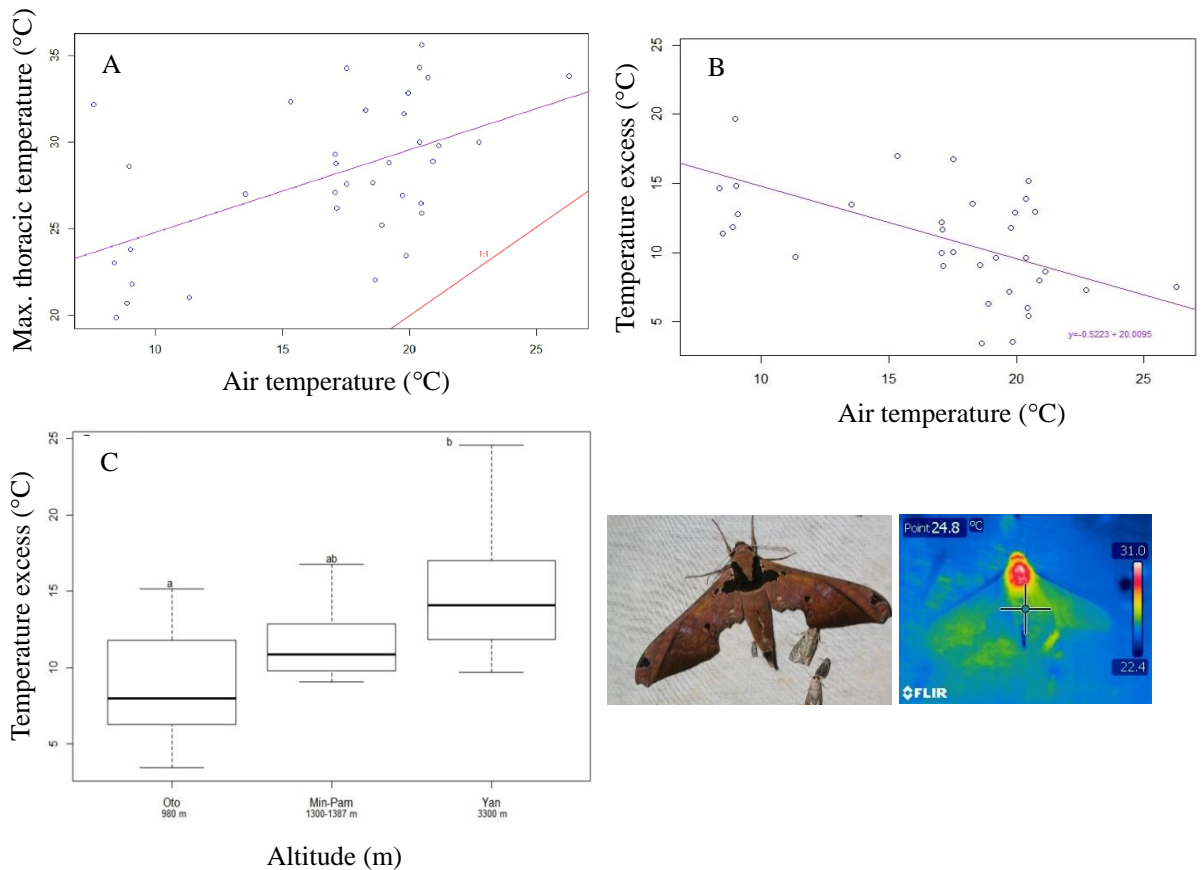
**Figure 14.** Photo (gauche) et image thermographique (droite) de la fleur dioïque de l'*Arum italicum* à Tours (en haut) et du bourgeon floral mâle du palmier *Tagua* (*Phytelephas aequatorialis*) en Equateur. La thermogénèse de la fleur de l'*Arum* a été assez bien étudiée : la chaleur est produite pendant seulement quelques heures en fin d'après midi pendant plusieurs jours afin d'attirer et de retenir le pollinisateur. La production de chaleur par le palmier, en revanche, était assez méconnue. De façon surprenante, seuls les bourgeons produisent de la chaleur tandis que les fleurs montrent plus tard une production assez mineure.

En 2016, avec le support d'un stage de M1, j'ai amorcé l'étude de fleurs thermogéniques dans un contexte de microclimat particulier pour les insectes pollinisateurs. En Touraine, l'*Arum italicum* est abondant. La fleur de cette plante produit de la chaleur afin d'attirer et de retenir les insectes pollinisateurs (des petits diptères) (Fig. 14). Nous avons dans un premier temps décrit le pattern de production de chaleur de la fleur sur plusieurs jours, à la fois sur le terrain et sous serre avec des plantes en pots. Les températures florales peuvent monter jusque 10-15°C au-dessus de la température de l'air. Sachant que les pollinisateurs restent dans la fleur pendant 24h, ces températures peuvent jouer un rôle dans l'écologie thermique des insectes. Le résultat le plus marquant est un changement dans le moment de la production de

chaleur durant la journée en fonction de la température environnementale : un réchauffement pourrait induire une production de chaleur plus tôt dans la journée. Ce résultat est important potentiellement car les insectes pollinisateurs peuvent également avoir une fenêtre d'activité restreinte durant la journée. Malheureusement nous manquons de connaissances sur l'écologie des insectes en question (Pshycoda). J'ai soumis un projet à l'ANR fin 2016 sur cette thématique, projet qui sera resoumis en 2019.

### ► *Le cas des insectes nocturnes endothermes*

En 2016, dans le contexte d'un stage de M2 avec une étudiante Equatorienne, et en collaboration avec Dr. Olivier Dangles (DR IRD), j'ai amorcé une étude sur la biologie thermique des insectes nocturnes endothermes. Les sphinx (papillons nocturnes) doivent monter en température, en produisant de la chaleur métabolique, pour pouvoir voler (Fig. 15). Nous avons réalisé une étude sur le terrain, dans les Andes en Equateur, afin de déterminer la capacité à monter en température en fonction de l'altitude (et donc de la température environnementale). Ces papillons sont capables de maintenir une température thoracique relativement constante le long du gradient d'altitude, suggérant une production de chaleur métabolique plus importante à haute altitude pour maintenir un écart avec l'air ambiant plus élevé qu'à basse altitude (Fig. 15). Puis nous avons testé au laboratoire, expérimentalement, dans quelle mesure la température et la quantité de nourriture ingérée durant les stades larvaires pouvaient influencer la capacité de l'adulte à générer suffisamment de chaleur métabolique pour atteindre une température thoracique permettant le vol. Les résultats montrent en particulier que la température durant le stade larvaire permet à l'adulte d'être acclimaté à des températures élevées et de monter plus rapidement en température. Toutefois, les sphinx montrent une grande capacité à atteindre et maintenir une certaine température thoracique malgré les effets importants de la température et de la nourriture larvaire sur la masse corporelle des adultes. Ces résultats nécessitent d'être approfondis pour identifier les drivers environnementaux de la capacité d'endothermie chez ces insectes.



**Figure A.1.15.** *Ecologie thermique des Sphinx. (A) Température thoracique maximale des papillons en fonction de la température de l'air le long du gradient d'altitude dans les Andes Equatoriennes. (B) Excès de température de leur thorax (différence avec la température de l'air) en fonction de la température de l'air. (C) Box plot des excès de température thoracique en fonction de l'altitude. A haute altitude, dans le froid, les sphinx montrent un écart de température plus élevé avec l'air ambiant que les papillons à basse altitude.*

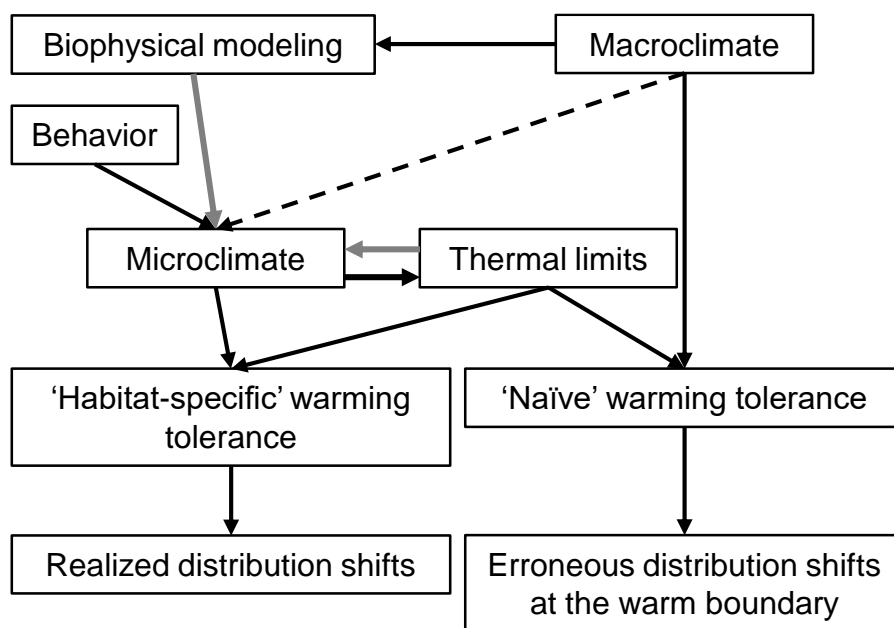
## 1.6 Mes apports aux questions sociétales (INEE)

Mes travaux génèrent des éléments de réponse à deux grandes questions sociétales qui sont centrales aux activités de l'INEE : (i) l'impact du changement climatique sur la biodiversité et (ii) la biologie de la conservation dans un contexte de changement global. Je contribue également à améliorer nos connaissances sur l'état actuel de la biodiversité à l'échelle de la région.

### ► *Le rôle du microclimat dans la réponse de la biodiversité au changement climatique*

Mes études se placent dans un contexte de l'impact du changement climatique sur les ectothermes. Mon approche consiste avant tout à développer des outils

prédictifs et à démontrer comment le microclimat des organismes peut moduler les effets potentiels du réchauffement. Mes études montrent le rôle clé du microclimat dans la réponse de la biodiversité de façon générale (Fig. 16). Des erreurs de prédiction importantes sont malheureusement attendues lorsque le microclimat est négligé lors de la prédiction des changements d'aire de distribution des organismes en réponse aux changements environnementaux. En particulier pour des organismes de petite taille comme les insectes qui peuvent vivre dans des microhabitats bien distincts de ce qui est mesuré par nos stations météorologiques. Evidemment, le microclimat de la vaste majorité des insectes est inconnu ou non quantifié. Et déployer des dataloggers partout dans l'espace sur le long terme est difficilement envisageable. L'alternative est donc de développer des modèles biophysique qui produisent des prédictions de température microclimatique (Fig. 16). Mes études soulèvent également un problème de design expérimental lors de la mesure des seuils de tolérance à la température des ectothermes (CTmax typiquement). En effet, ces protocoles doivent se baser sur la dynamique microclimatique (ex : taux de montée en température par minute, durée d'exposition à la température expérimentale) pour obtenir des CTmax réalistes et pertinents dans le contexte prédictif.



**Figure 16.** Diagramme conceptuel montrant la démarche pour étudier la tolérance au réchauffement des ectothermes. Parce que nous manquons cruellement d'informations sur le microclimat de la majorité des espèces, la tolérance au réchauffement est souvent déduite à partir de la température atmosphérique (approche 'naïve'). Cette approche naïve génère des informations erronées sur les changements de distribution des espèces qui sont surestimés ou sous-estimés si le microhabitat amplifie ou gomme les températures maximales environnementales, respectivement. Au contraire, en utilisant les températures microclimatiques et des informations sur la thermorégulation comportementale, nous pouvons prédire la tolérance au réchauffement de façon plus juste et réaliste. Voir Pincebourde and Casas, *Ecology*, 2015.

### ► *Biologie de la conservation dans un climat changeant*

J'aborde la problématique de la biologie de la conservation avec mon approche microclimatique, en particulier sur le modèle Odonates. L'objectif est de jouer sur les microclimats pour conserver le patrimoine biologique. Nous étudions en effet des espèces rares et menacées (ex : leucorrhines). Les plans de conservation sont en général établis à une échelle assez large, typiquement en agissant sur l'ensemble des berges d'une pièce d'eau ou bien en restaurant intégralement une zone humide. Mes projets aquatiques viennent compléter ces aspects en identifiant quel niveau d'hétérogénéité spatiale est nécessaire pour optimiser les chances de maintien de ces espèces sensibles dans un climat toujours plus variable et changeant. Les résultats scientifiques fondamentaux générés par les projets en cours seront transférés aux gestionnaires des zones sensibles afin de discuter sur les modalités possibles pour maximiser les probabilités de maintiens de conditions optimales pour les populations de ces libellules.

Un autre aspect, abordé notamment dans le projet Région PROTECTODO, est d'analyser à quel point le patrimoine culturel peut servir pour conserver le patrimoine naturel. De nombreux châteaux de la Loire ont des zones aquatiques dans leur parc avec des stratégies d'entretien plus ou moins développées. Ces parcs abritent parfois une biodiversité exceptionnelle, au point que certaines espèces rares et menacées (ex : libellules) parviennent à se maintenir grâce à ces zones. De plus, ces châteaux peuvent servir d'outils de communication avec le grand public, qui s'y déplace nombreux, sur les questions relatives à la biodiversité. L'APR Intelligence des Patrimoines est un support important pour ce type de projet en Région Centre Val de Loire.

### ► *Etat des lieux de la biodiversité régionale*

*Document de synthèse* : Baeta R., Sansault E. et **Pincebourde S.**, 2012. Déclinaison régionale du Plan National d'Actions en faveur des Odonates en région Centre 2013-2017. Association Naturaliste d'Étude et de Protection des Écosystèmes « Caudalis » / Institut de Recherche sur la Biologie de l'Insecte / Direction Régionale de l'Environnement, de l'Aménagement et du Logement Centre, 112 pp.

Les plans de conservation sont efficaces seulement si nos connaissances sur l'état de santé des populations sont suffisantes. En 2011, le Ministère de l'Écologie, de l'Énergie, du Développement durable et de la Mer lançait le Plan National d'Actions en faveur des Odonates (libellules et demoiselles menacées). Ce plan couvre la période 2011-2015, et consiste à définir des actions de protection, de gestion, de formation et de sensibilisation visant les espèces Odonates les plus menacées sur notre territoire français. Ce plan permet en outre d'approfondir nos connaissances sur l'état des populations Odonates en France, ainsi que sur la biologie et l'écologie de ces espèces. Ce plan national a été décliné au niveau des 22 régions (ancien découpage du territoire). J'ai été le coordinateur régional (chargé de mission

en région Centre) de cette déclinaison du PNA en 2011-2012, sous la tutelle de la DREAL Centre. A ce titre, j'ai co-rédigé cette déclinaison régionale (Plan Régional d'Actions) qui consiste à établir une synthèse de nos connaissances sur l'état des populations des espèces ciblées par le plan national (8 espèces sur les 18 ciblées par le plan national sont présentes en région Centre). La région Centre est un « hot spot » de la diversité odonotologique en France grâce à la grande diversité de milieux aquatiques dans cette région. Aussi, j'ai mis au point, en lien étroit avec les acteurs principaux de la protection des Odonates (associations naturalistes, gestionnaires des réserves et des parcs, agences publiques), des actions détaillées et spécifiques pour la période 2011-2015. Ces actions doivent permettre d'améliorer considérablement nos connaissances et le statut des populations Odonates visées. L'ensemble de ce travail se fait en partenariat étroit avec l'association naturaliste ANEPE Caudalis (Renaud Baeta et Eric Sansault). Lien web : <http://odonates.pnaopie.fr/plans-regionaux/centre/>

## 2 – Enseignement, Formation, et Diffusion

### ► Encadrement d'une thèse

*Étudiant* : Robin Caillon (IRBI).

*Intitulé* : Biogéographie du microclimat foliaire : mécanismes et conséquences dans les relations plante-arthropode.

*Type de financement* : bourse ministérielle.

*Période* : Thèse soutenue le 29/01/2016.

*Codirection* : Prof. Christelle Suppo (10%) et Dr. Sylvain Pincebourde (90%, non HDR).

*Mon implication* : Ce sujet de thèse est adossé directement à mes propres intérêts scientifiques (voir descriptif dans la partie scientifique ci-dessus). Tandis que mon projet ANR MicroClimMite se focalise sur les échelles spatiales de la feuille et de la canopée, le sujet de Robin Caillon correspond à l'échelle biogéographique des interactions plante-microclimat-organismes. Ce sujet découle de mes propres réflexions conceptuelles. La Prof. Christelle Suppo est intervenue dans un chapitre de la thèse axé sur l'analyse spatialisée des déplacements d'acariens à la surface des feuilles. La thèse a abouti à une publication (*Functional Ecology* 2014), un manuscrit est soumis et un 3ème article est prévu. Robin Caillon n'a pas souhaité poursuivre en recherche académique, et est actuellement sur un poste de Data Analyste dans le privé.



### ► Participations à l'enseignement

J'interviens dans des modules au niveau Master (1 et 2) et dans 3 établissements différents, pour un volume annuel d'environ 30 heures. Mes enseignements correspondent à mes thématiques de recherche.

- Interventions dans le *Master 2 "Agronomie et Agroécologie"* à AgroParis Tech (Paris) chaque année depuis 2010. Les interventions sont de 3 heures / an. Contact: Marie Odile Bancal. Intitulé du cours : Biophysique environnementale des relations plante-insecte.
- Enseignements en *Master à l'Université François Rabelais* depuis 2013. Contact : Elisabeth Huguet.

**Master 1** "Biologie Intégrative", 10 heures (2h CM + 8h TD), intitulé des cours : écologie thermique des organismes dans un climat changeant.

**Master 2** "Ecologie Comportementale, Evolution et Biodiversité", 12 heures (6h CM + 6h TD), intitulé des cours : écologie thermique des organismes.

- Intervention depuis 2016 dans *Master 2 "Forêt et Mobilisation des Bois"* à l'Université d'Orléans (4hrs/an). Contact : Régis Fichot. Intitulé du cours : Interactions biophysiques au sein des canopées.

### ► Formation professionnelle

- Intervenant chaque année depuis 2015 pour la formation « L'eau, de la Loire au Laboratoire » (*Maison pour la Science*, à destination des enseignants du second degré), en qualité de formateur sur la Biodiversité liée aux milieux aquatiques.
- Organisation en 2014, à l'IRBI, de 2 *sessions de formation* sur l'écologie et la systématique des Odonates, destinées aux acteurs de la conservation des habitats des Odonates, en collaboration avec l'association naturaliste ANEPE Caudalis.

### ► Vulgarisation et diffusion

Je contribue de façon modeste à la vulgarisation de mes travaux, en particulier via 3 articles de vulgarisation :

- Paez E.V., Pincebourde S., Montufar R. & Dangles O. (2016) Una flor endotérmica en los Andes del Ecuador. *Nuestra Ciencia* n°18, pp8-11. ISSN: 1390-1893.
- Pincebourde S., Lazzari C.R. & Boulay R. (2015) Les insectes et leurs adaptations à la température. *Microscop* (ed. CNRS délégation centre Poitou-Charentes), hors-série 2015, pp. 26-27. ISSN 1247-844X.
- Pincebourde S. Encart sur le projet ANR MicroCliMite (2013). "Uncovering the mysteries of microclimate impacts". *International Innovation - Disseminating science, research and technology* (ResearchMedia Ltd), numéro d'août 2013, pp82-84.

Mon activité de diffusion vers le grand public est bien plus marquée :



- Animation d'un atelier sur la biologie des libellules à la Maison de la Loire (37) en 2016, à destination du grand public (nombre de participants: 15).
- Participation à un débat-conférence sur le changement climatique en marge de la COP21, organisée par la SEPANT en 2015 à Tours, en tant qu'expert biodiversité.
- Participation au Train du Climat en 2015, animation d'un stand sur l'impact des changements climatiques sur les insectes.
- Conférence grand public en 2015 « Du changement climatique et des insectes dans mon jardin » dans le cadre de la fête de la Science.
- Intervention dans un module de l'École Doctorale de l'Université François Rabelais (2012), organisé par l'association des doctorants (ADOCT): « préparation au concours de la fonction publique » (4 heures). Mon intervention portait sur le concours CNRS.
- Animation d'une table ronde au 15<sup>ème</sup> forum sur l'insertion professionnelle des jeunes chercheurs, organisé par l'ADOCT à Tours (2012) : « Postdoc : quoi, quand et après ? » (1 jour).

### 3 – ENCADREMENT, ANIMATION ET MANAGEMENT DE LA RECHERCHE

#### ► Animation d'un programme national français

En 2011, le Ministère de l'Écologie, de l'Énergie, du Développement durable et de la Mer lançait le Plan National d'Actions en faveur des Odonates (libellules et demoiselles menacées). Ce plan couvre la période 2011-2015, et consiste à établir des actions de protection, de gestion, de formation et de sensibilisation visant les espèces Odonates les plus menacées sur notre territoire français. Ce plan permet en outre d'approfondir nos connaissances sur l'état des populations Odonates en France, ainsi que sur la biologie et l'écologie de ces espèces. Ce plan national a été décliné au niveau des 22 régions françaises (structure du territoire avant la mise en place des nouvelles régions).

J'ai été le coordinateur régional (chargé de mission en région Centre) de cette déclinaison du PNA, sous la tutelle de la DREAL Centre. A ce titre, j'ai coordonné la rédaction en 2012 de cette déclinaison régionale (Plan Régional d'Actions, lien web : <http://odonates.pnaopie.fr/plans-regionaux/centre/>) qui consiste à établir une synthèse de nos connaissances sur l'état des populations des espèces ciblées par le plan national (8 espèces sur les 18 ciblées par le plan national sont présente en région Centre). La région Centre est un « hot spot » de la diversité odonatologique en France, en particulier avec les populations importantes du Parc Naturel Régional de la Brenne et des espèces associées aux grands fleuves (Loire, Cher). Cette rédaction a été faite en lien étroit avec les acteurs principaux de la protection des Odonates (associations naturalistes, gestionnaires des réserves et des parcs, agences publiques). L'ensemble de ce travail s'est fait en partenariat étroit avec l'association naturaliste ANEPE Caudalis (Président : Renaud Baeta). **Cette déclinaison a abouti au montage du projet Od'SPOT en 2013, en partenariat avec l'association naturaliste, et financé par le Fondation LISEA pour la Biodiversité, qui notamment remporté en 2014 le Trophée du mécénat décerné par le Ministère de l'Ecologie. Dans la foulée, ce travail a généré le projet PROTECTODO, financé par la région Centre Val de Loire (2015-2018) et toujours en partenariat avec l'association naturaliste. Je coordonne ces 2 projets de recherche.**

#### ► Animation et management de projets de recherche

Entre 2012 et 2016, j'ai été ou suis le coordinateur principal de 4 programmes de recherche.

J'ai été le coordinateur principal du projet **MicroClimite** (ANR Blanc ; 2011-2015; 240 k€). A ce titre j'ai coordonné les efforts de recherche entre les 2 partenaires (IRBI et INRA PIAF à Clermont Ferrand). Ce projet intègre des expérimentations en laboratoire et sur le terrain ainsi que de la modélisation, ce qui demande une coordination particulière entre les différents acteurs qui agissent dans ces 3 étapes. En 2012, j'ai recruté sur ce contrat un Ingénieur d'Étude (Amélie Ezanic) à l'IRBI, que j'ai formé sur différents aspects expérimentaux du projet (écologie thermique), en interaction avec le doctorant Robin Caillon. J'ai moi-même contribué à chaque étape scientifique du projet qui a généré un total de 10 articles scientifiques (d'autres sont à venir).

Je suis le coresponsable du projet **OD'SPOT** (2013-2017: Biologie de la conservation des Odonates dans un climat changeant; fondation LISEA pour la Biodiversité; 50 k€), en partenariat étroit avec l'association naturaliste ANEPE Caudalis. Je suis plus particulièrement le responsable de la partie recherche fondamentale du projet tandis que l'association gère les aspects liés à la constitution d'un atlas des espèces Odonates en région Centre. Cette association originale entre un laboratoire de recherche fondamentale et une association naturaliste, financé par un organisme privé, nous a permis d'obtenir le Trophée du Mécénat en 2013.

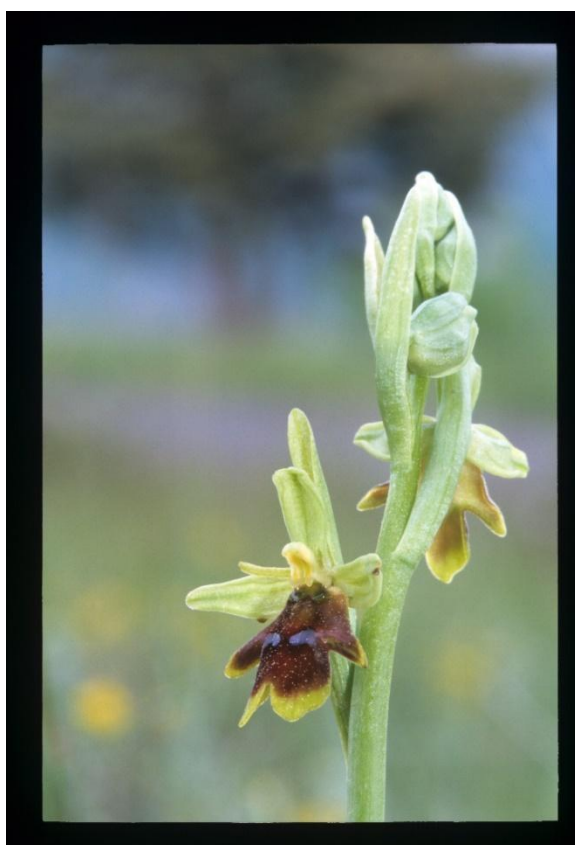
Je suis le coordinateur du projet **PROTECTODO** (2015-2018 : biologie de la conservation des Odonates dans un climat changeant; Financé par la Région Centre; 206 k€) qui se combine avec le projet OD'SPOT cité ci-dessus. A ce titre, je coordonne les tâches réalisées par moi-même, l'Ingénieur d'Etude (Aurélia Le Naour) recrutée sur le projet, et les deux partenaires (association naturaliste et UMR CITERES). Je coordonne également les efforts de valorisation du projet dans le cadre du programme Intelligence des Patrimoines (IPAT), afin de montrer le rôle du patrimoine culturel (parcs des châteaux de la Loire) dans la conservation des Odonates.

Enfin, je coordonne un programme **PICS** (CNRS) qui officialise mes relations avec le Prof Arthur Woods à l'Université du Montana (USA) (Projet **MEGAleaf**, modélisation du microclimat foliaire à l'échelle globale ; 20k€ demandés mais ~7k€ financés). La flexibilité de ce programme PICS me permet de gérer et de combiner de façon judicieuse avec d'autres financements pour des mobilités entre les 2 laboratoires afin de continuer nos travaux de modélisation du microclimat foliaire.



## *Appendix 2.*

### *Detailed curriculum vitae*



The European orchid *Ophrys aymonini*, a rare and iconic terrestrial orchid that I was lucky to find by chance. Photo: Sylvain Pincebourde.



## Physical ecology and integrative physiology

**SYLVAIN PINCEBOURDE**

Born on Dec 22, 1977, French

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**Current position:** CNRS Research Scientist (CRCN).

✉ **Laboratory:** Insect Biology Research Institute, IRBI, CNRS UMR 7261, Université de Tours, Parc Grandmont, 37200 Tours, France.

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☎ **Department fax:** +33 (0)2 47 36 69 66

**ResearchGate:** [https://www.researchgate.net/profile/Sylvain\\_Pincebourde](https://www.researchgate.net/profile/Sylvain_Pincebourde)

**Web page:** <https://sylvainpincebourde.wordpress.com/>

**Keywords:** Biophysical ecology; Biotic interactions; Climate change ecology; Microclimate; Thermal ecology; Thermoregulation.

### PROFESSIONAL POSITIONS

<b>Since 2017</b>	<b>Team leader</b> of the group INOV at IRBI.
<b>Since 2014</b>	CNRS Research Scientist (1st class), IRBI.
<b>2009-2013</b>	CNRS Research Scientist (2nd class), IRBI.

### UNIVERSITY EDUCATION

<b>2008-2009</b>	<b>Postdoctoral researcher</b> – PHYSICAL ECOLOGY OF PREY PREDATOR RELATIONSHIPS. <i>Laboratory Supervisor</i> Research Institute on Insect Biology (IRBI), Tours, France. Prof. Jérôme Casas ( <a href="mailto:jerome.casas@univ-tours.fr">jerome.casas@univ-tours.fr</a> ).
<b>2006-2007</b>	<b>Postdoctoral researcher</b> – FORECASTING THE IMPACTS OF CLIMATE CHANGES ON INTERTIDAL BIOTIC INTERACTIONS. <i>Laboratory Supervisor</i> University of South Carolina, Columbia, SC, USA. Prof. Brian Helmuth ( <a href="mailto:b.helmuth@neu.edu">b.helmuth@neu.edu</a> ).
<b>2002-2005</b>	<b>PhD thesis</b> – ENVIRONMENTAL BIOPHYSICS OF ENDOPHYTIC INSECTS. <i>Laboratory Supervisor</i> Research Institute on Insect Biology (IRBI), Tours, France. Prof. Jérôme Casas ( <a href="mailto:jerome.casas@univ-tours.fr">jerome.casas@univ-tours.fr</a> ).
<b>2001-2002</b>	<b>MSc degree</b> – BIOLOGY, EVOLUTION AND CONTROL OF POPULATIONS. University François Rabelais (Tours, France).

CURRENT PROJECTS AND FUNDING

PROJECTS AS PRINCIPAL INVESTIGATOR

<b>PICS (CNRS)</b>	2016-2018 – Project MEGAlaef, modelling the leaf microclimate at global scale. Funded by CNRS (20k€).
<b>Projet Région</b>	2015-2018 – Project PROTECTODO, Conservation biology of Odonata in a changing climate. Funded by the region Centre (206 k€).
<b>ANR Blanc</b>	2011-2015 – MicroCliMite project: Connecting global climate and microclimate. Funded by ANR.
<b>Od'SPOT</b>	2013-2017 – Od'SPOT project: Odonates, displacements, distribution and landscape structure, funded by LISEA Foundation for Biodiversity, co-PI (association ANEPE Caudalis).
<b>PRA Odonates</b>	2012-2015 – Regional declination (Centre) of the National Plan for Odonate species. Funded by DREAL.
<b>Invited Prof</b>	2012 – University François Rabelais, obtained funds for a temporary Professor (invited) position for Prof. Arthur H. Woods (University of Montana, USA).
<b>SPE INRA</b>	2011-2013 – Experimental study and biophysics of the greenhouse agrosystem, funded by SPE INRA. Co-PI (A. Bout, INRA Sophia-Antipolis).
<b>PEPS (INEE)</b>	2010 – Exploratory and Pluridisciplinary Programs funded by INEE (CNRS): project THERMALGAMES.

PROJECTS AS PARTICIPANT

<b>PHENEC</b>	2019-2023 - Role of phenology in species distribution and in their management in a changing climate. Funded by ANR, PI: Christelle Robinet (INRA URZF, Orléans).
<b>MODELISE</b>	2018-2021 – Modélisation de la distribution spatiale d'habitats favorables d'espèces cibles. Funded by Région Centre Val de Loire, PI: Francis Isselin Nondedeu (CITERES Univ Tours).
<b>CANOPEE</b>	2018-2021 – Biodiversité des insectes des canopées de chênes déperissants. Funded by Région Centre Val de Loire, PI: Aurélien Sallé (Univ Orléans).
<b>CAREX</b>	2017-2020 – Restauration des tourbières, CARbone du sol & biodiversité: indicateurs issus de l'EXpérimentation. Funded by Région Centre Val de Loire, PI: Fatima Laggoun (ISTO/OSUC Orléans).
<b>SEPTOVAR</b>	2014-2015 – Responses of local populations of <i>Mycosphaerella graminicola</i> to spatial variations in temperature and host plant resistance, and the potential for adaptation to climate change, Funded by BASC (INRA), PI: Frédérique Suffert (INRA Grignon).
<b>AgroEco</b>	2013-2015 – AgroEco project, Pest management through biodiversity conservation in agro-forestry. Funded by Region Centre, PI: Prof. Jérôme Casas (University of Tours).



- SNB** 2012-2015 – Project from the National Strategy for Biodiversity: Restoration of ecological continuum in wetlands and peatlands of the Chinon forest (37), PI: Francis Isselin (University of Tours).

#### PRIZES AND MEDIA COVERAGE

##### PRIZES

- **‘Exceptional reviewer’ among Springer journals** (for *Oecologia* in 2017).
- **‘Highly cited article’** in Web of Science (Potter, Woods and Pincebourde, *Global Change Biology* 2013) in 2015, 2016, 2017 and 2018.
- **Trophy for corporate sponsorship** (Ministry for Ecology, 2013) for the project Od'SPOT.
- Nominated as among the 10 « **Top Referees 2010** » by the journal *Biology Letters*.
- **Elton Prize 2008** for the best article published by a young investigator in the *Journal of Animal Ecology* in 2007 (British Ecological Society).

#### REVIEWING ACTIVITIES

**Associate Editor** for the international peer-reviewed journal *The American Naturalist* since July 2018.

**Handling Editor** for the international peer-reviewed journal *Oecologia* since January 2014. Member of the committee selecting the recipient of the *Hanski award* every year.

**Guest Editor** (Pincebourde & Woods) for the international peer-reviewed journal *Current Opinion in Insect Science* in 2019-2020. Special topic: Global Change Biology.

**Guest Editor** (Woods, Dillon, Pincebourde & Terblanche) for the international peer-reviewed journal *Advances in Insect Physiology* in 2019-2020. Special topic: Extended phenotypes.

**Guest Editor** (Giron, Dubreuil & Pincebourde) for the international peer-reviewed journal *Entomologia Experimentalis et Applicata* in 2017. Special issue: Insect-Plant Interactions.

**Guest Editor** (Lajeunesse & Pincebourde) for the international peer-reviewed journal *Science of the Total Environment* in 2018/2019. Special issue: Climate Change and Water.

##### **Reviewer for 68 international peer-reviewed journals:**

My page on Publons: <https://publons.com/author/1179212/sylvain-pincebourde#profile>)

-*Category ‘Ecology’*: Ecology Letters; Ecological Monographs; The American Naturalist; Functional Ecology; Journal of Animal Ecology; Oecologia; Oikos; Methods in Ecology and Evolution; Journal of Applied Ecology; Biotropica; Plant Ecology; Ecology and Evolution; Ecological Modelling; Ecological Informatics; BMC Ecology; Microbiol Ecology.

-Category 'Entomology': Journal of Insect Physiology; Entomologia Experimentalis et Applicata; Agricultural and Forest Entomology; Journal of Applied Entomology; Environmental Entomology; European Journal of Entomology; Acarologia; Annales de la Société Entomologique de France; Biological Control; International Journal of Pest Management; Insect Science; Pest Management Science; Bulletin of Insectology.

-Category 'Biology': Proceedings Royal Soc B; Interface; Biology Letters; Biological Bulletin; Jordan Journal of Biological Sciences; CR Biologies; Journal of Thermal Biology; BMC Evolutionary Biology; Annals of Applied Biology; The Open Biotechnology Journal; Heliyon.

-Category 'Multidisciplinary Sciences': Nature Ecology and Evolution; Plos One; African Journal of Agricultural Research; Oxford Bibliographies.

-Category 'Zoology': Animal Behavior; Integrative and Comparative Biology; Journal of Comparative Physiology B; Comparative Biochemistry and Physiology A.

-Category 'Environmental Sciences': Global Change Biology; Conservation Physiology; Ecological Indicators; Biodiversity and Conservation; Frontiers of Biogeography; Sustainability; Agriculture, Ecosystems and Environment; Journal of Soil and Water Science.

-Category 'Meteorology and Atmospheric Sciences': Climate Dynamics.

-Category 'Plant Sciences': New Phytologist; Plant Methods.

-Category 'Oceanography': Limnology and Oceanography.

-Category 'Marine and Freshwater Biology': Marine Ecology Progress Series; Journal of Experimental Marine Biology and Ecology; Marine Biology; Canadian Journal of Fisheries and Aquatic Sciences; Journal of Molluscan Studies.

-Category 'Horticulture': Scientia Horticulturae.

-Category 'Instruments and Instrumentation': Quantitative InfraRed Thermography Journal.

#### **Reviewer for funding agencies:**

2019 – ERC starting grant / Région Aquitaine DR08 / NRF South Africa / National Science Centre Poland / MacArthur Fellowship / Czech Science Foundation.

2018 – Graduate School for Production Ecology and Research Conservation (PE&RC, The Netherlands).

2017 – National Science Foundation (NSF).

2015 – Grant Competition FONDECYT (CONICYT, Chili) / Fonds de la Recherche Scientifique – FRS-FNRS (Belgique) / GIS Réseau francilien de recherche sur le développement soutenable R2DS / DIM ASTREA (call for PhD proposals).

2014 – Expertise for the French Ministry of Ecology, sustainable development and energy, program APR2014-Pesticides-Ecophyto.

2009 – National Science Foundation (NSF).

**Member of the 'Nature Reader Panel' [2010-2011].**

#### ORGANIZATION OF EVENTS AND PARTICIPATION TO COMMITTEES

**Principal organizer of the international workshop HETEROCLIM** (Loches, 10-14 June, 2014): the response of organisms to climate change in heterogeneous environments.

**Co-organizer of the workshop « Thermal ecology » in Ecuador** (Quito, Ecuador, 24-25/06/2015), Funded by the Universidad Catholica de Quito.

**Co-organizer of the CC&W2018 international conference** in Tours, France (5-7 Feb 2018): Diversity of local responses to the impacts of climate change on water.

#### **Member of the Organization Committee:**

- For the annual meeting of the French Ecological Society (SFE, Paris, 20/09/2010).

- For the 18th Conference on Insect Biology (Tours, France, 20-24/06/2016).
- For the 16th Symposium on Insect-Plant Interactions (Tours, France, 1-5/07/2017).

**Executive committees:**

2016-2018 – Member of the Scientific Advisory Board of the GENOMITE project (H2020 program).

Since 2014 – Correspondent for the lab in the network RTP MIDI "The rendez-vous of habitats and diversity for a sustainable management of natural resources and biodiversity".

Since 2013 – Member of the Departmental Commission for Wildlife, landscapes and sites.

Since 2013 – member of the executive committee of the network EPIARCH (Epidemiology and Architecture).

Since 2010 – member of the 'Commission Scientifique Disciplinaire Paritaire (CSDP)' at the University of Tours.

At IRBI – Member of financial committee, Member of the PhD Thesis commission.

## TEACHING AND TRAINING

**Supervision of PhD students:** [2011-2015] Co-supervision of Robin Caillon on the biogeography of the leaf microclimate. Defended on 29/01/2016.

**Supervision of students** – Research Institute on Insect Biology.

2019 – Sophie Lenoir, Master 2 (University Aix-Marseille).

2017 – Nicolas Meyer, Master 2 (AgroSup Dijon / University of Bourgogne).

2016-2018 – Aurélie LeNaour, Engineer (CNRS).

2016 – Erika Paez, Master 2 (University of Tours / Universidad Catholica Quito).

2015 – Camille Vonnet, Master 1 (University of Tours).

2015 – Elodie Pineau, Master 2 (University of Poitiers).

2014 – Thomas Cahon, Master 1 (University of Tours).

2013 – Doriane Muller, Master 2 (University of Loraine).

2013 – Déborah Auclair, Master 1 (Univ Tours).

2011 – Robin Caillon, Master 2 (AgroParis Tech, Paris).

2011 – Tom Ratz, Licence 1 (Univ Tours).

2008 – Antoine Morisot, Licence 3 (Univ Tours).

2003 – Sophie Delaide, Master 1 (Univ Tours).

**PhD thesis assessments:**

2019 – *Reviewer* of the PhD Thesis of Oscar Franken, University of Groningen (NL).

2018 – *Reviewer* of the PhD Thesis of Zac Hemmings, University of New England (Australia).

2019 – *Examination* of the PhD Thesis of David Rozen-Rechels, University Sorbonne.

2018 – *Examination* of the PhD Thesis of Joaquin Soler, University of Tours.

2017 – *Examination* of the PhD Thesis of Estefania Quenta, University of Tours.

2016 – *Examination* of the PhD Thesis of Robin Caillon, Université of Tours.

2015 – *Examination* of the PhD Thesis of Emile Faye, Université Paris 6 / IRD.

2012 – *Examination* of the PhD Thesis of Greg P.A. Lamarre, University of Antilles-Guyana (INRA ECOFOR, French Guyana).

- 2013/2015 – *President* of the PhD committee of Emile Faye (IRD and University de La Paz, Bolivia).
- 2018 – *Committee member* of the PhD committee of Marta Zaffaroni (Supervisor Daniele Bevacqua, INRA PSH Avignon).
- 2017 – *Committee member* of the PhD committee of Victoria Dahlhoff (Supervisor Arthur Woods, University of Montana).
- 2017 – *Committee member* of the PhD committee of Estefania Quenta (Supervisor Olivier Dangles, IRD).
- 2016/2017 – *Committee member* of the PhD committee of Anne-Lise Boixel (Supervisor Frédéric Suffert, INRA Paris Grignon).
- 2015/2017 – *Committee member* of the PhD committee of Alice Denis (Supervisor Laurent Pélozuelo, ECOLAB, University Toulouse).
- 2015/2016 – *Committee member* of the PhD committee of Lucile Muneret (Supervisor: Adrien Rush, INRA SAVE, Bordeaux).
- 2010-2012 – *Committee member* of the PhD committee of Frédéric Bernard (INRA Paris- Grignon, France).

#### **Hiring committees:**

- 2019 – President of the hiring committee for a "Maitre de Conférence" position at the University of Tours
- 2018 – Member of the hiring committee for a "Maitre de Conférence" position at the Bordeaux SciencesAgro unit.

#### **Teaching**

- Since 2015 – Training program on « Water, from the Loire river to the laboratory » (Maison pour la Science, for teachers), expertise on biodiversity. 2 days / year.
- Since 2013 – University François Rabelais; Master 2 Behavioural Ecology, Evolution and Biodiversity (12 hours); Master 1 Integrative Biology (10 hours).
- 2017 – Training program on « Biodiversity: from the field to the laboratory and the classroom » (Maison pour la Science, for teachers), expertise on biodiversity. 2 days / year.
- 2014 – Organization of 2 training sessions on the ecology and systematics of Odonata, for policy makers, co-organized with the naturalist association ANEPE Caudalis.
- 2016-2018 – University of Orléans; Master 2 Forests (4 hours/year).
- 2010-2016 – Master 2 Agronomy and Agroecology, AgroParis Tech (4 hours/year).
- 2003-2004 – University François Rabelais, Licence 3: Statistics in ecology (25 hours), Animal and vegetal ecology (70 hours).

## PUBLICATIONS

*INTERNATIONAL JOURNALS (42 PUBLICATIONS)* [Index-h: 22 \(Google Scholar\)](#)

[2019]

- Porras M.F., Navas C.A., Marden J.H., Mescher M.C., De Moraes C.M., **Pincebourde S.**, Sandoval-Mojica A., Raygoza-Garay J.A., Holguin G.A., Rajotte E.G. & Carlo T.A. Enhanced heat tolerance of virus-infected aphids leads to niche expansion and reduced interspecific competition. **Nature Communications**, in revision.

- Yun T., Cao L., An F., Chen B., Xue L., Li W., **Pincebourde S.**, Smith M.J. & Eichhorn M.P. Simulation of multi-platform LiDAR for assessing total leaf area in tree crowns. **Agricultural and Forest Meteorology**, 276-277, 107610 (in press).
- Koussoroplis A.M., Klauschies T., **Pincebourde S.**, Giron D. & Wacker A. A comment on “Variability in plant nutrients reduces insect herbivore performance”. **Rethinking Ecology**, 4, 79–87.
- **Pincebourde S.** & Casas J. Narrow safety margin in the phyllosphere during thermal extremes. **PNAS**, 116, 5588–5596.
- LeNaour A., Baeta R., Sansault E., Deville M. & **Pincebourde S.** Telemetry reveals the habitat selected by immature dragonflies: implications for conservation of the threatened dragonfly *Leucorrhinia caudalis* (Odonata: Anisoptera). **Journal of Insect Conservation**, 23, 147–155.

[2018]

- Woods H.A., Saudreau M. & **Pincebourde S.** Structure is more important than physiology for estimating intra-canopy distributions of leaf temperatures. **Ecology and Evolution**, 8, 5206–5218.
- Quenta E., Casas J., Dangles O. & **Pincebourde S.** Temperature effects on ballistic prey capture by a dragonfly larva. **Ecology and Evolution**, 8, 4303–4311.
- Giron D., Dubreuil G. & **Pincebourde S.** Special Issue: 16th International Symposium on Insect-Plant Relationships: Preface. **Entomologia Experimentalis et Applicata**, 166, 317–318. *Special issue: Insect-plant interactions.*
- Giron D., Dubreuil G., Bennet A., Dedeine F., Dicke M., Dyer L., Erb M., Harris M.O., Huguet E., Kaloshian I., Kawakita A., Lopez-Vaamonde C., Palmer T.M., Petanidou T., Poulsen M., Sallé A., Simon J-C., Terblanche J.S., Thiéry D., Whiteman N., Woods H.A., Zchori-Fein E. & **Pincebourde S.** Promises and challenges in insect–plant interactions. **Entomologia Experimentalis et Applicata**, 166, 319–343. *Special issue: Insect-plant interactions.*
- Cahon T., Caillon R. & **Pincebourde S.** Do aphids alter leaf surface temperature patterns during early infestation? **Insects**, 9, 34.

[2017]

- Saudreau M., Ezanic A., Adam B., Caillon R., Walser P. & **Pincebourde S.** Temperature heterogeneity over leaf surfaces: the contribution of the lamina microtopography. **Plant, Cell & Environment**, 40, 2174–2188.
- Koussoroplis A.M., **Pincebourde S.** & Wacker A. Understanding and predicting physiological performance of organisms in fluctuating and multifactorial environments. **Ecological Monographs**, 87, 178–197.
- **Pincebourde S.**, van Baaren J., Rasmann S., Rasmont P., Rodet G., Martinet B. & Calatayud P.-A. Plant-Insect Interactions in a Changing World. In N. Sauvion, P.-A. Calatayud & D. Thiéry (Volume Eds), **Advances in Botanical Research** series: Vol 81. Insect-Plant Interactions in a Crop Protection Perspective (pp. 289-332). Elsevier, GBR.

[2016]

- **Pincebourde S.**, Montúfar R., Paez E. & Dangles O. The discovery of heat production by an Ecuadorian palm. **Frontiers in Ecology and the Environment**, 14, 571–572.



- **Pincebourde S.**, Murdock C.C., Vickers M. & Sears M.W. Fine-scale microclimatic variation can shape the responses of organisms to global change in both natural and urban environments. **Integrative and Comparative Biology**, 56, 45–61. *Special issue: Beyond the Mean: Biological Impacts of Changing Patterns of Temperature Variation.*
- **Pincebourde S.** & Suppo C. The vulnerability of tropical ectotherms to warming is modulated by the microclimatic heterogeneity. **Integrative and Comparative Biology**, 56, 85–97. *Special issue: Beyond the Mean: Biological Impacts of Changing Patterns of Temperature Variation.*
- Dillon M.E., Woods H.A., Wang G., Fey S.B., Vasseur D.A., Telemeco R.S., Marshall K. & **Pincebourde S.** Life in the frequency domain: the biological impacts of changes in climate variability at multiple time scales. **Integrative and Comparative Biology**, 56, 14–30. *Special issue: Beyond the Mean: Biological Impacts of Changing Patterns of Temperature Variation.*
- **Pincebourde S.** & Casas J. Hypoxia and hypercarbia in endophagous insects: Larval position in the plant gas exchange network is key. **Journal of Insect Physiology**, 84, 137–153. *Special issue: Plant reprogrammers.*
- Faye E., Dangles O. & **Pincebourde S.** Distance makes the difference in thermography for ecological studies. **Journal of Thermal Biology**, 56, 1–9.

[2015]

- Woods H.A., Dillon M.E. & **Pincebourde S.** The role of microclimatic diversity and of behavior in mediating the responses of ectotherms to climate change. **Journal of Thermal Biology** 54, 86-97. *Special issue: What sets the limit? How thermal limits, performance and preference in ectotherms are influenced by water or energy balance.*
- Casas J., Body M., Gutzwiller F., Giron D., Lazzari C.R., **Pincebourde S.**, Richard R., & Llandres A.L. Increasing metabolic rate despite declining body weight in an adult parasitoid wasp. **Journal of Insect Physiology** 79, 27–35.
- **Pincebourde S.** & Casas J. Warming tolerance across insect ontogeny: influence of joint shifts in microclimates and thermal limits. **Ecology** 96, 986–997.

[2014]

- Caillon R., Suppo C., Casas J., Woods A.H., & **Pincebourde S.** Warming decreases thermal heterogeneity of leaf surfaces: implications for behavioural thermoregulation by arthropods. **Functional Ecology** 28, 1449–1458.

[2013]

- Potter K., Woods A.H. & **Pincebourde S.** Microclimatic challenges in global change biology. **Global Change Biology** 19, 2932–2939.
- **Pincebourde S.**, Sanford E. & Helmuth B. Survival and arm abscission are linked to regional heterothermy in an intertidal sea star. **Journal of Experimental Biology** 216, 2183-2191.
- Morice S., **Pincebourde S.**, Darboux F., Kaiser W. & Casas J. Predator-prey pursuit-evasion games in structurally complex environments. **Integrative and Comparative Biology** 53, 767–779.
- Saudreau M., **Pincebourde S.**, Dassot M., Adam B., Loxdale H.D. & Biron D.G. On the canopy structure manipulation to buffer climate change effects on insect herbivore development. **Trees – Structure & Function** 27, 239-248.

[2012]

- **Pincebourde S.**, Sanford E., Casas J. & Helmuth B. Temporal coincidence of environmental stress events modulates predation rates. **Ecology Letters** 15, 680-688.
- **Pincebourde S.** & Woods A.H. Climate uncertainty on leaf surfaces: the biophysics of leaf microclimates and their consequences for leaf-dwelling organisms. **Functional Ecology** 26, 844-853. *Virtual Issue: Ecophysiological forecasting: predicting adaptation and limits to adaptation.*
- Fly E.K., Monaco C.J., **Pincebourde S.** & Tullis A. The influence of intertidal location and temperature on the metabolic cost of emersion in *Pisaster ochraceus*. **Journal of Experimental Marine Biology and Ecology** 422-423, 20-28.

[2009]

- **Pincebourde S.**, Sanford E. & Helmuth B. An intertidal sea star adjusts thermal inertia to avoid extreme body temperatures. **The American Naturalist** 174, 890-897.
- Sinoquet H., **Pincebourde S.**, Adam B., Donès N., Phattaralerphong J., Combes D., Ploquin S., Sangsing K., Kasemsap P., Thanisawanyangkura S., Groussier-Bout G. & Casas J. 3-D maps of tree canopy geometries at leaf scale. **Ecology** 90, 283. Datapaper.

[2008]

- **Pincebourde S.**, Sanford E. & Helmuth B. Body temperature during low tide alters the feeding performance of a top intertidal predator. **Limnology and Oceanography** 53, 1562-1573.
- Théry M., **Pincebourde S.** & Feer F. Dusk light environment optimizes visual perception of conspecifics in a crepuscular horned beetle. **Behavioral Ecology** 19, 627-634.

[2007]

- **Pincebourde S.**, Sinoquet H., Combes D. & Casas J. Regional climate modulates the canopy mosaic of favourable and risky microclimates for insects. **Journal of Animal Ecology** 76, 424-438. *Elton Prize winner (BES).*

[2006]

- **Pincebourde S.** & Casas J. Multitrophic biophysical budgets: thermal ecology of an intimate herbivore insect-plant interaction. **Ecological Monographs** 76, 175-194.
- **Pincebourde S.**, Frak E., Sinoquet H., Regnard J.L. & Casas J. Herbivory mitigation through increased water use efficiency in a leaf mining moth-apple tree relationship. **Plant, Cell and Environment** 29, 2238-2247.
- **Pincebourde S.** & Casas J. Leaf miner-induced changes in leaf transmittance cause variations in insect respiration rates. **Journal of Insect Physiology** 52, 194-201.

[2005]

- Casas J., **Pincebourde S.**, Mandon N., Vannier F., Poujol R. & Giron D. Lifetime nutrient dynamics reveal simultaneous capital and income breeding in a parasitoid. **Ecology** 86, 545-554.



- Feer F. & **Pincebourde S.** Diel flight activity and ecological segregation within an assemblage of tropical forest dung and carrion beetles. **Journal of Tropical Ecology** 21, 21-30.
- Van Loon J.J.A., Casas J. & **Pincebourde S.** Nutritional ecology of insect-plant interactions: persistent handicaps and the need for innovative approaches. **Oikos** 108, 194-201.

[2004]

- Giron D., **Pincebourde S.** & Casas J. Lifetime gains of host-feeding in a synovigenic parasitic wasp. **Physiological Entomology** 29, 436-442.

*BOOK CHAPTERS:*

Brun L., Parisi L., **Pincebourde S.** & Saudreau M. (2020) L'anticipation des impacts du changement climatique sur les bio-agresseurs en arboriculture fruitière. In *Adaptation des productions fruitières au changement climatique* (Ed JM Legave). **QUAE**.

*JOURNALS WITHOUT PER-REVIEWS (VULGARISATION):*

Paez E.V., **Pincebourde S.**, Montufar R. & Dangles O. (2016) Una flor endotérmica en los Andes del Ecuador. *Nuestra Ciencia* n°18, pp8-11.

**Pincebourde S.**, Lazzari C.R. & Boulay R. (2015) Les insectes et leurs adaptations à la température. **Microcoop** (ed. CNRS délégation centre Poitou-Charentes), hors-série 2015, pp. 26-27. ISSN 1247-844X.

Encart sur le projet ANR MicroCliMite (2013). "Uncovering the mysteries of microclimate impacts". **International Innovation - Disseminating science, research and technology** (ResearchMedia Ltd), numéro d'août 2013, pp82-84.

**Pincebourde S.** (2010) Écologie du changement climatique: la biophysique s'en mêle. **Microcoop** (ed. CNRS délégation centre Poitou-Charentes) n°13, hors-série Biodiversité, pp.22-23. ISSN 1247-844X.

*PUBLIC DOCUMENT:*

**Pincebourde S.** & Casas J., 2017. Adaptations des insectes au changement climatique. In: *Les mécanismes d'adaptation de la biodiversité aux changements climatiques et leurs limites* (Eds. S. Lavorel, J-D. Lebreton & Y. Le Maho). **Rapport de l'Académie des Sciences**, pp.53-58.

Baeta R., Sansault E. et **Pincebourde S.**, 2012. Déclinaison régionale du Plan National d'Actions en faveur des Odonates en région Centre 2013-2017. Association Naturaliste d'Étude et de Protection des Écosystèmes « Caudalis » / Institut de Recherche sur la Biologie de l'Insecte / **Direction Régionale de l'Environnement, de l'Aménagement et du Logement Centre**, 112 pp.

## COMMUNICATIONS

### INVITED ORAL COMMUNICATIONS (14)

Workshop on the non-climatic dimension of climate refugia (11/2018, Bordeaux, **France**). *Finding a refuge to climate change: Biophysical processes at small scale matter?*

Annual meeting of the Entomological Society of America, Symposium: Insect Microclimates in a Changing World (11/2017, Denver, CO, **USA**). *Thermal ecology of insect herbivores: A biophysical view of the insect-plant interface.*

Seminar series of the MIDI network: Thematic Network of Research on Habitats and Diversity (10/05/2016, Orléans, **France**). *The key role of microclimates in the response of organisms to climate change.*

SICB Annual Meeting, Symposium: Beyond the mean: Biological impacts of changing patterns of temperature variation (2-7/01/2016, Portland, Oregon, **USA**). *The thermal heterogeneity at leaf, canopy and biogeographical scales: consequences for leaf dwelling insects.*

Le STUDIUM Conference, Insects, pathogens, and plant reprogramming: from effector molecules to ecology (5-7/11/2015, Tours, **France**). *Physical and physiological reprogramming of plants by insects: consequences in a changing climate.*

Conférence invitée à l'Université Catholique de Quito (2/2015, Quito, **Equateur**). *The role of microclimates in mediating climate changes: ecological consequences.*

Invited seminar at the University of Montana (11/2014, Missoula, **USA**). *The role of microclimates in mediating climate changes.*

International workshop on stochastic weather generators SWGEN (17-19/09/2014, Avignon, **France**). *The role of microclimates in climate change responses: ecologists need climatic data with high resolution.*

International workshop HETEROCLIM, The response of organisms to global change in heterogeneous environments (10-14/06/2014, Loches, **France**). *Ecological implications of the mismatch between macro- and micro-climates in ectoterms.*

Seminar series of the Trinity College, conférence invitée par Ian Donohue (12/2012, Dublin, **Irlande**). *Biotic interactions in fluctuating microclimates: Experimenting, modelling and predicting climate change impacts.*

Conférence invitée à l'INRA Grignon, invité par Michaël Chelle (05/2012, Grignon, **France**). *Microclimats, environnements fluctuants et performance des organismes : importance des interactions temporelles.*

Annual Meeting of the British Ecological Society (09/2008, London, Imperial College, **Royaume Uni**). *Ecological impacts of climate changes: biophysics reveals the mechanisms.*

Center for Insect Sciences, conférence invitée à University of Arizona (11/ 2007, Tucson AZ, **USA**). *Environmental biophysics of a leaf mining insect.*

John and Mary Louise Seminar Series UC Davis, conférence invitée (7/ 2006, Bodega Marine Lab, **USA**). *Thermal ecology of an intimate herbivore insect – plant relationship.*

### ORAL COMMUNICATIONS (27)

Sfécologie-2018, International Conference of Ecological Sciences (10/2018, Rennes, **France**). *Living in the leaf microclimate: herbivory modifies leaf temperature patterns.*

Séminaire d'échanges entre chercheurs, concepteurs et gestionnaires: concevoir et gérer des villes favorables à la nature (11/2018, Blois, **France**). *Le microclimat des insectes et des plantes: quel rôle dans la conception urbaine?*

SIP16- 16th Symposium on Insect Plant Interactions (2-5/07/2017, Tours, **France**). *Extended phenotypes and global change biology.*

Sfécologie-2016, International Conference of Ecological Sciences (24-27/10/2016, Marseille, **France**). *Warming tolerance across insect ontogeny: influence of joint shifts in microclimates and thermal limits.*

Colloque d'Eco-Physiologie Animale, 2ème édition CEPA (4-6/11/2015, La Rochelle, **France**). *Warming tolerance across insect ontogeny: influence of joint shifts in microclimates and thermal limits.*

Annual Meeting of the Society for Experimental Biology (SEB; 1-4/07/2014, Manchester, **UK**). *Insects in changing climates: the challenges of integrating microclimates and behavioral thermoregulation into realistic predictions.*

International workshop HETEROCLIM, 'The response of organisms to climate change in heterogeneous environments' (10-14/06/2014, Loches, **France**). *A global model of leaf microclimates during climate change: implications for insect performance.*

Annual Meeting of the Society for Integrative and Comparative Biology (SICB) (01/2013, San Francisco, **USA**). *Microclimatic research priorities that will improve our predictions of the effects of climate change.*

97th Annual Meeting of the Ecological Society of America, ESA (08/2012, Portland, OR, **USA**). *Temporal coincidence of environmental stress events modulates predation rates.*

Conference on Plant and Canopy Architecture Impact on Disease Epidemiology and Pest Development, ECA (7/2012, Rennes, **France**). *Ecological impacts of climate changes: biophysics reveals mechanisms at the canopy scale + Thermal ecology of spider mites at the leaf surface.*

2nd Annual meeting of the European PhD Network in Insect Sciences (10/2011, Joué les Tours, **France**). *From Global to micro-climate changes: Biophysics reveals buffering mechanisms + Thermal ecology of spider mites at the leaf surface.*

Annual Meeting of the American Physiological Society, 'Global change & global science: comparative physiology in a changing world' (08/2010, Westminster, CO, **USA**). *Ecological impacts of climate changes: biophysics reveals the mechanisms.*

Annual Meeting of the Society for Experimental Biology (07/2008, Marseilles, **France**). *Interaction between underwater and aerial body temperatures in influencing a top predator feeding rate in the intertidal.*

Western Society of Naturalists – Annual meeting (11/2007, Ventura CA, **USA**). *Environmental variations and keystone predator performance in the intertidal.*

Western Society of Naturalists – Annual meeting (11/2006, Redmond WA, **USA**). *Thermal stress alters feeding rate in a keystone predator.*

Entomologentagung in Dresden (3/2005, Dresden, **Germany**). *Making the best of mother's choice: use of the mine microhabitat by a leaf miner.*

VIIeme Journées d'Ecologie Fonctionnelle (3/ 2005, Super-Besse, **France**). *Ecologie thermique d'une relation intime entre un insecte herbivore et sa plante hôte.*

European PhD Course in Insect Biotechnology: Insect Signalling and Interactions (10/2004, Maratea, **Italy**). *The thermal environment of a phyto-endophagous insect.*

SIP 12 – Symposium Insect-Plant Relationships (8/2004, Berlin, **Germany**). *Take over of stomatal control by a leaf mining insect.*

European PhD Course in Insect Biotechnology: Insect-Plant Interactions (5/2004, Capri, **Italy**). *Take over of stomatal control by a leaf mining insect.*

ACI Ecologie Quantitative (12/2003, Tours, **France**). *Le microclimat d'un insect vivant à l'intérieur d'un vegetal.*

Forum NATRIX-association for naturalists- (12/2003, Tours, **France**). *Evolutionary Biology of temperate orchids: hybridisation matters.*

Association for Tropical Biology and Conservation, and the British Ecological Society: Biotic Interactions in the Tropics (7/2003, Aberdeen, **UK**). *Physical ecology of ambient light constraints colour signalling in birds and horned beetles.*

Colloque de la Société Française d'Etude du Comportement Animal (4/2003, Tours, **France**). *Coloration corporelle et signalisation visuelle honnête chez un scarabée à corne de Guyane Française.*

GDR Ecologie Comportementale (9/2002, Dijon, **France**). *Sélection de l'habitat lumineux chez des bousiers Phanaeini (Coleoptera, Scarabaeidae) de forêt primaire en Guyane française.*

#### *POSTER COMMUNICATIONS (13)*

Conference 'Our common Future under climate change' (7-10/07/2015, Paris, **France**). *Warming tolerance across insect ontogeny: influence of joint shifts in microclimates and thermal limits.*

BES-SFE Joint Annual Meeting (11/2014, Lille, **France**). *Warming tolerance across insect ontogeny: influence of joint shifts in microclimates and thermal limits.*

International workshop HETEROCLIM, 'The response of organisms to climate change in heterogeneous environments' (10-14/06/2014, Loches, **France**). Title 1: *Linking leaf microclimate to leaf performance along a latitudinal gradient.* Title 2: *Distance makes the difference in thermography for ecological studies.* Title 3: *Modelling spatial and temporal leaf temperature dynamics at leaf and canopy scales.* Title 4: *The development of a fungal pathogen is affected by daily fluctuations of leaf temperature.*

7th international conference on FSPM (Functional-Structural Plant Models, Saariselkä, **Finland**, 9-14/06/2013). *Modelling spatial and temporal leaf temperature dynamics-A focus on the leaf boundary layer.*

Séminaire Biodiversité Ligérienne (Tours, 06/2011, **France**). *Premier atlas des Odonates d'Indre-et-Loire : un projet liant chercheurs et naturalistes.*

SIP14, 14th Symposium on Insect-Plant Interactions (Wageningen, 08/2011, **Netherlands**). *Thermal ecology of a spider mite at the leaf surface.*

11<sup>th</sup> International Behavioral Ecology Congress (7/2006, Tours, **France**). *Colour signalling to conspecifics in a horned beetle.*

Jacques-Monod seminars (CNRS) on the Physico-Chemical Ecology of organisms (9/2005, Roscoff, **France**). *Multitrophic biophysical budgets: Thermal ecology of an intimate herbivore insect-plant interaction.*

Annual Meeting of the Society for Experimental Biology (7/2005, Barcelona, **Spain**). *Multitrophic biophysical budgets: Thermal ecology of an intimate herbivore insect-plant interaction.*

Summer School on Biodiversity and Species Interactions (10/2003, Neuchâtel, **Switzerland**). *Thermal regime, canopy geometry and prey-predator interactions.*