
The impact of short-term extreme temperature on Swiss biodiversity

Internship at “MaLeFiX” project of WSL Research Programme
“Extremes 2021-2024”

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Introduction

Climate change is altering global temperature and precipitation patterns, making the alpine ecosystem particularly vulnerable due to its biota being generally limited by low temperatures (Vanneste et al., 2017; Trenberth, 2011). As a result of rising temperatures and decreasing summer precipitation (Mazdiyasni & AghaKouchak, 2015), extreme weather events such as heatwaves, droughts, floods, wildfires, and storms have become more intense and frequent (Kron et al., 2019). For example, the severe heatwave that occurred in Europe during the summer of 2003 caused 70,000 fatalities and a 30% loss of gross primary production of terrestrial ecosystems (Kron et al., 2019). In addition, the lack of precipitation provides ideal conditions for wildfires to spread, leading to the destruction of forests and threatening lives. The wildfires that occurred during the heatwaves in 2003 and 2010 caused losses of more than \$1.2 billion in southern Europe and \$2 billion in Russia (Kron et al., 2019). Without preparation for these climate change-triggered natural hazards, an increasing number of people and other organisms on this planet will face the challenge of survival.

Extreme weather events are drivers of broad biological responses to climate trends. Short-term periods of several days exceeding species-specific temperature thresholds can lead to dramatic changes in physiology, reproduction, and even cause the death of individuals (Easterling et al., 2000; Ma et al., 2015). For example, changes in the incidence of extreme temperatures could result in a highly skewed population sex ratio in turtles (Bull & Vogt, 1979). Chronic exposure to high temperatures may induce male sterility in *Drosophila* (Rohmer et al., 2004). Although temperature patterns are computed on a linear scale, species' responses to temperature are generally not linear, since metabolic rates increase exponentially with temperature (Dillon et al., 2010), and acclimation may buffer heat stress (Buckley & Huey, 2016).

The fitness consequences of heat stress vary among regions and taxa. It is predicted that organisms living at mid to high latitudes in the Northern Hemisphere are most affected by climate warming due to the rapidly rising temperatures in these regions (Parmesan, 2007; Root et al., 2003; Rosenzweig et al., 2008). Although the magnitude of the temperature rise

is relatively small in the tropics, the deleterious effects of extreme events should not be underestimated, since species in these regions are currently living very close to their optimal temperature, and a small-scale warming event can substantially reduce their fitness (Deutsch et al., 2008).

Ectotherms, such as fish and amphibians, are particularly vulnerable to climate warming as their physiological functions heavily depend on ambient temperatures (Paaïmans et al., 2013). Their thermal tolerance is characterized by a nonlinear, asymmetric curve (Fig. 1) that connects the optimum temperature (T_{opt}), the critical minimum temperature (CT_{min}), and the critical maximum temperature (CT_{max}), which indicate the direct effect of temperature on organism fitness (Deutsch et al., 2008; Paaïmans et al., 2013). In contrast, most endotherms, such as birds and mammals, are able to maintain a relatively constant body temperature, even under extreme climate conditions (Scholander, 1955). However, they need to expend additional energy to make behavioral, morphological, and physiological adjustments for thermoregulation when the environmental temperature falls below or above their comfort zone, ultimately reducing their fitness over prolonged periods (Oswald et al., 2011).

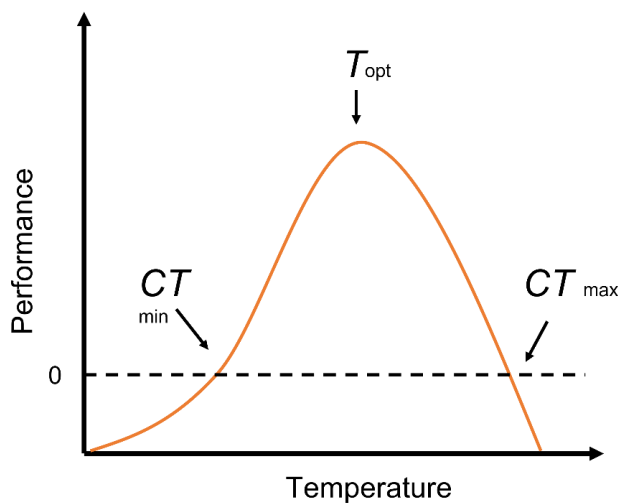


Figure 1 Thermal performance curve. The curve illustrates the relationship between temperature and the ability of ectotherms to perform their basic physiological functions. It rises gradually at the beginning with temperature from a minimum critical temperature CT_{min} to an optimum temperature T_{opt} and then drops rapidly to a critical thermal maximum, CT_{max} .

Critical thermal limits play a crucial role in estimating the impacts of climate change on organisms. Biologists have developed and refined standard protocols to quantify the thermal stress level of animals. Critical thermal maximum (CT_{max}), introduced by Cowles & Bogert

(1944) as "*the thermal point at which locomotory activity becomes disorganized and the animal loses its ability to escape from conditions that will promptly lead to its death*" is a commonly used and essential measure of an ectotherm's upper thermal tolerance limit. CT_{max} can be defined experimentally by increasing the environmental temperature until animals lose muscle control or fall into a heat coma (Cowles & Bogert, 1944; Cox, 1974; Lutterschmidt & Hutchison, 1997).

For endotherms, their thermal tolerance ranges are defined by the concept of the thermal neutral zone (TNZ), which is a range of ambient temperatures where birds and mammals can maintain their internal temperature with minimal metabolic regulation (Kingma et al., 2014). Experimental measurements of TNZ provide an estimate of the long-term thermal tolerance of endothermic species (Khaliq et al., 2014). Livestock, such as domesticated mammals, suffer from heat stress when their body temperature increases with inadequate heat dissipation, resulting from an elevated ambient temperature above TNZ, along with high humidity and slow air movement (Wang et al., 2020). Therefore, the temperature-humidity index (THI) is a calculated index that accounts for the combined effects of environmental temperature and relative humidity. This index was first introduced to describe the comfort level of ambient temperature in humans (Thom, 1959) and then adapted to describe environmental conditions that drive heat stress in dairy cattle and other livestock (Armstrong, 1994; Noordhuizen, 2017; Sarangi, 2018; Wang et al., 2020).

Deductive and inductive approaches have been developed to model the climatic niche of terrestrial and aquatic biota (Grünig et al., 2020). Inductive methods, such as species distribution models (SDMs), correlate species occurrence records with environmental data to infer the conditions that are suitable for species in the future (Elith & Leathwick, 2009; Guisan & Thuiller, 2005). However, the correlative approach of SDMs has been criticized for not considering the physiological processes behind species range shifts (Kearney et al., 2010; Lawler et al., 2006). In contrast, the deductive approach adopted in physiological models takes into account the biological process behind the species' response to the changing environment, allowing for more confident predictions of species' response (Cooke et al., 2013; Gamliel et al., 2020; Kearney et al., 2010). A simple form of these models utilizes physiological limits like thermal thresholds obtained in the experiment to predict species distribution (Martínez et al., 2015).

The objective of this study is to establish a link between extreme weather events and ecosystem services using a simplified physiological modelling approach. To achieve this, we gathered and compiled information on species' thermal tolerance constraints from previous literature, which we combined with environmental conditions as input data to predict the risk from temperature extremes on vertebrate species of the Swiss fauna over the next 14 days. While sub-seasonal forecasts of weather-related hazards such as drought and flood have been helpful to many end-users (Cao et al., 2021; Vitart et al., 2017), no similar approach has been taken to forecast biodiversity risks. Our goal is to bridge this gap in sub-seasonal weather-biodiversity prediction, enabling timely conservation decision-making ahead of imminent heat wave events in Switzerland. As the climate continues to change, it is critical that we develop effective tools and strategies to protect and conserve the world's biodiversity. Our study represents a step towards achieving this goal, by providing a practical and useful tool for predicting and mitigating the impacts of extreme weather events on vertebrate species.

Methods

Compilation of critical thermal limits

We gathered thermal tolerance data for various species from a variety of sources, including databases and literature. One of the databases we used was the GlobTherm database, which was created by Bennett et al. (2018) and contains experimentally derived thermal tolerance data for both aquatic and terrestrial organisms. Additionally, we utilized data from Morley et al. (2019), who conducted long-term experiments on 319 marine polar species to measure their critical thermal maxima (CTmax). Comte and Olden (2017) compiled upper thermal limits for 485 fish species and predicted the CTmax for 2960 freshwater and marine fish species using a data imputation approach based on phylogenetic niche conservatism. In addition, Khaliq et al. (2014) provided information on the endothermic thermal neutral zone (TNZ) for 255 bird species and 297 mammal species. From these large databases, we extracted data on the critical thermal limits of species that are found in Switzerland.

For some groups of species, such as amphibians and livestock, we were unable to locate sufficient data in the aforementioned databases. In these cases, we reviewed individual

studies focused on these species to obtain their thermal tolerance data directly from the physiological studies.

Physiological response model

We investigated the potential effects of extreme weather events on species development and fitness by using meteorological variables as input. To do so, we implemented a physiological model to calculate the suitability of the ambient temperature of Swiss terrestrial and aquatic species (Grünig et al., 2020).

The model calculates a critical temperature index (CT_i) by comparing the species' upper thermal limit (CT_{max} for ectotherms and the upper boundary of the thermal neutral zone (UTNZ) for endotherms) with the ambient temperature. For fish and mammals, we calculate the number of days where the daily maximum temperature surpasses their upper thermal limit. For livestock, we investigate whether the temperature-humidity index (THI) exceeds the pre-defined mild, moderate, and severe stress levels for cattle, sows, and horses.

$$CT_i = \frac{\sum_{k=1}^n p_k}{n}$$

Where

$$p_k = \begin{cases} 1 & \text{if } T_{max,k} > CT_{max} \\ 0 & \text{if } T_{max,k} \leq CT_{max} \end{cases} \quad \text{for fish and mammals}$$

$$p_k = \begin{cases} 1 & \text{if } THI_k > THI_{severe} \\ 0.5 & \text{if } THI_{severe} > THI_k > THI_{moderate} \\ 0.2 & \text{if } THI_{moderate} > THI_k > THI_{mild} \end{cases} \quad \text{for livestock}$$

Since the impact of heat stress depends on its intensity and duration (Rezende et al., 2014), we calculate CT_i as an accumulation of critical conditions over the past 14 days. The result of CT_i is a value between 0 and 1, indicating the susceptibility of species to extreme weather. A value close to 1 means the species' upper thermal limit has been crossed for most of the days, and the species suffers from chronically unsuitable environmental conditions. A value equal

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to 0 indicates the species has been living in a comfortable environment, and their thermal threshold has not been crossed for any day in the past half-month. For livestock, the value of CT_i is also determined by how many degrees its physiological limit has been crossed. We applied the physiological model to two case studies.

For terrestrial ecosystems, we selected three sub-catchments in the canton of Zurich, Valais, and Ticino. We used the climate variables from the summer of 2003, which is believed to be one of the hottest summers in Europe in the past 500 years (Luterbacher et al., 2004), large numbers of heat-related deaths were reported (Kovats et al., 2004). The summer of 2003 had a non-negligible impact on ecosystems, with extensive loss of livestock, wilted crops, and loss of forest cover (UNEP, 2004).

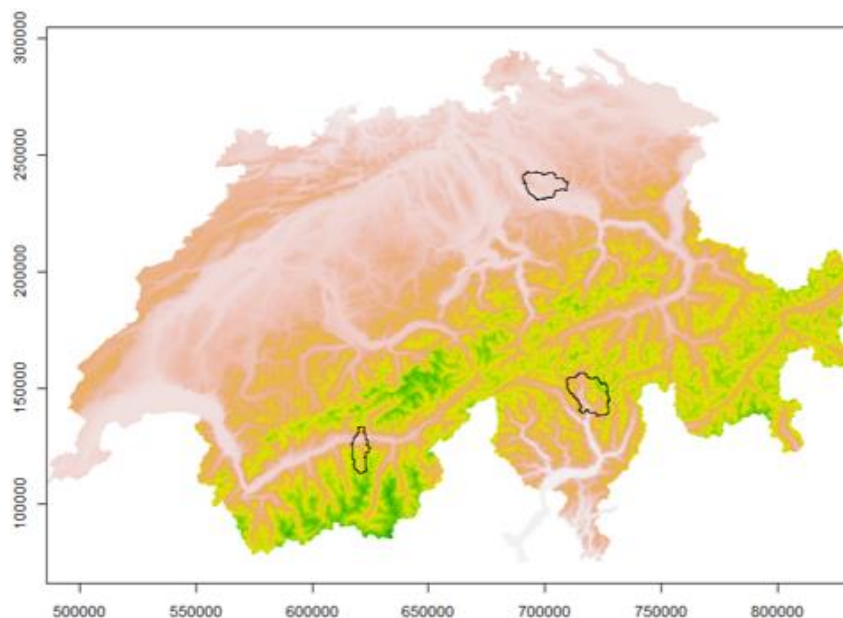


Figure 2 Sub catchments selection. This plot shows the three sub-catchments we selected for the case study in the canton of Zurich, Valais, and Ticino.

To test whether high temperatures and humidity crossed their critical threshold temperatures, we selected three mammals (muskrat, red fox, and wolf) and three common livestock (cattle, sows, and horses) in Switzerland. We chose red foxes and wolves as they are apex predators that can influence ecosystems in profound ways (Wallach et al., 2015). Muskrats were chosen because they are invasive species in Switzerland, and their relocation may damage canal banks, dikes, and ditches, leading to floods (Reinhardt et al., 2003). We calculated their critical

temperature index (CT_i) in the summer of 2003 to test whether their critical threshold temperatures are crossed by high temperatures and humidity.

Climate data acquisition

We obtained daily maximum and mean temperatures and relative humidity data from MeteoSwiss (www.meteoswiss.admin.ch) for terrestrial ecosystems. These meteorological observations and forecasts had a spatial resolution of 500m x 500m and served as inputs for our physiological model. However, since MeteoSwiss did not provide us with daily water temperature data, we had to use remote sensing data and point measurements to approximate water temperature for aquatic ecosystems.

To achieve this, we combined country-wide available remote sensing data with point measurements of water temperature from BAFU ($n=XX$) to derive satellite brightness temperature from the thermal bands of Landsat 8, using Google Earth Engine. We only used water temperature measurements from BAFU monitoring stations located in stream segments wider than the spatial resolution of Landsat 8's thermal infrared bands (30 meters) to perform a simple linear regression between the measured data and the brightness temperature from Landsat 8. This linear relationship was then used to correct remote sensing data for extensive areas apart from the monitoring stations in Switzerland.

As Landsat 8 orbits the earth every 16 days, daily temperature readings were not available from remote sensing data. Thus, we used mean temperature data from 2014 to 2021 for summer and winter to perform linear regression. For our case study, we selected two river segments in areas with high summer temperatures: one located in River Rhone and the other on the river Doubs. We obtained their maximum and mean temperature in summer 2018 and ran a 30-day simulation to mimic the process of water temperature linearly increasing from seasonal mean temperature to the highest temperature and then falling back to the average temperature in a month.

Results

Data Records

We have compiled thermal tolerance tables for 87 species, including 57 fish, 11 amphibians, 15 mammals, and 4 livestock species in Switzerland. For ectotherms, we obtained CT_{max} as the upper thermal threshold, while for endotherms, we used the upper TNZ limit.

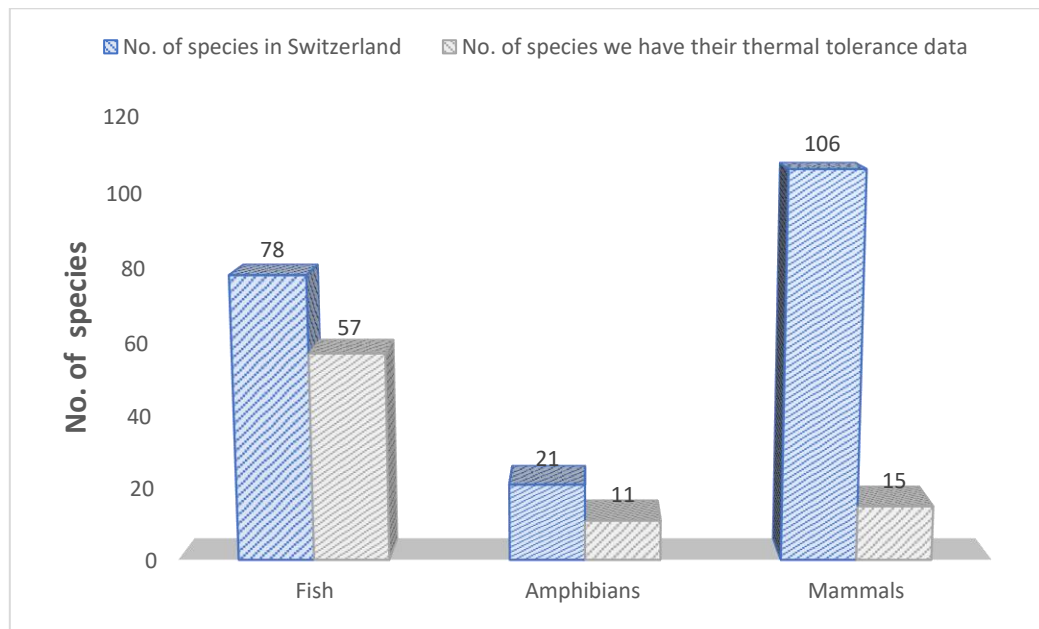


Figure 3 Summary statistics for data synthesis. The plot shows the total number of fish, amphibians, and mammals we have in Switzerland and the number of species that we got their critical thermal limits through literature review.

Case study for terrestrial ecosystems

The temperature patterns in the three sub-catchments were found to be quite similar. However, there were more variations in air temperature in Zurich and Valais, with Zurich experiencing the greatest number of days with maximum temperatures above 30°C. Although the mean temperature in Ticino was warmer than the other two sub-catchments most of the time, the maximum temperature here was not as high as in Zurich.

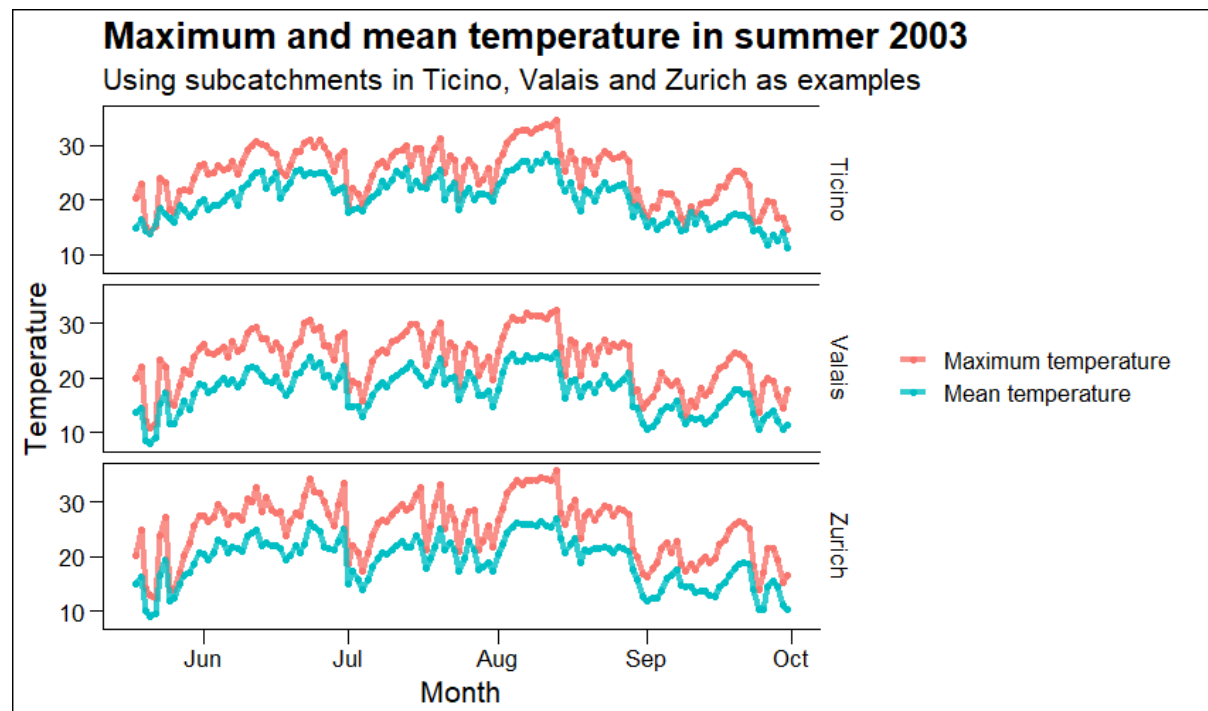
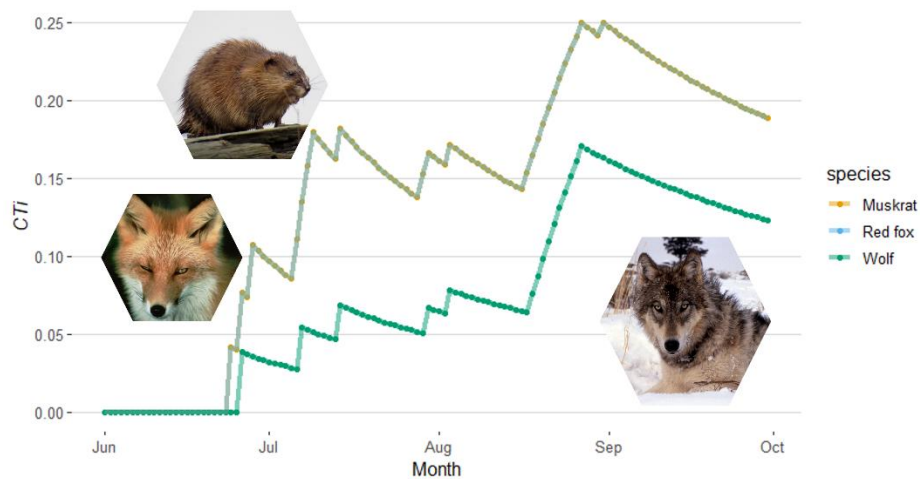


Figure 4 Temperature variations in three sub-catchments in Ticino, Valais, and Zurich. The plot shows how the maximum and mean temperatures vary in the three sub-catchments from June to September 2003.

We found that most species in the three sub-catchments, except for wolves in Valais, experienced some degree of heat stress from extreme weather events. Red foxes and muskrats were found to be less tolerant of high temperatures compared to wolves, while horses were found to be more sensitive to high temperature and humidity compared to cattle and sows. Zurich was found to be the least comfortable region for animals, with higher CT_i values being reached there. However, all the calculated CT_i values were below 0.25, indicating that the adverse effects of extreme weather on mammals and livestock in these areas were mild.

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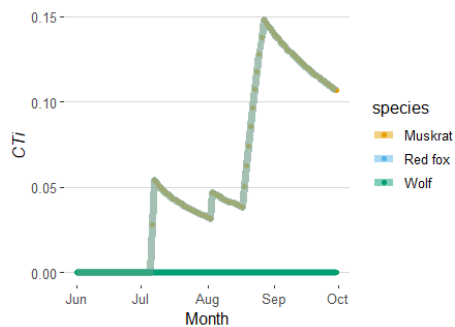
A1 CTi for mammals in subcatchment of Zurich



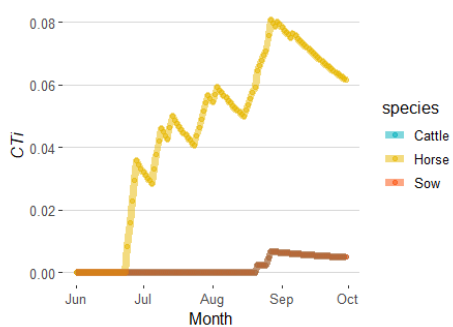
A2 CTi for livestock in subcatchment of Zurich



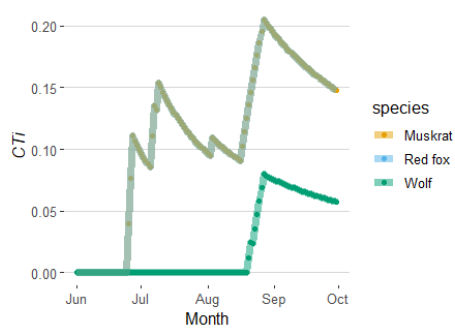
B1 CTi for mammals in subcatchment of Valais



B2 CTi for livestock in subcatchment of Valais



C1 CTi for mammals in subcatchment of Ticino



C2 CTi for livestock in subcatchment of Ticino

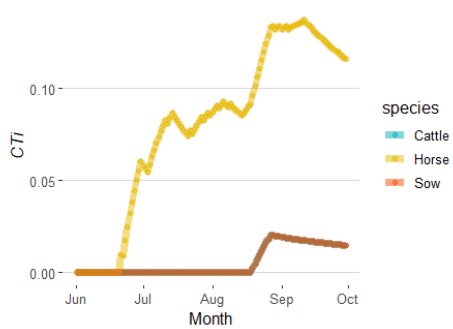


Figure 5 Critical temperature index for mammals and livestock in three sub-catchments. (A1) mammals in Zurich; (A2) livestock in Zurich; (B1) mammals in Valais; (B2) livestock in Valais; (C1) mammals in Ticino; (C2) livestock in Ticino.

Case study for aquatic ecosystems

The water temperature data that we extracted from winter and summer showed very different patterns. As this project focused more on the impact of heatwaves and drought on species fitness, we chose to calibrate the linear model based solely on summer temperatures.

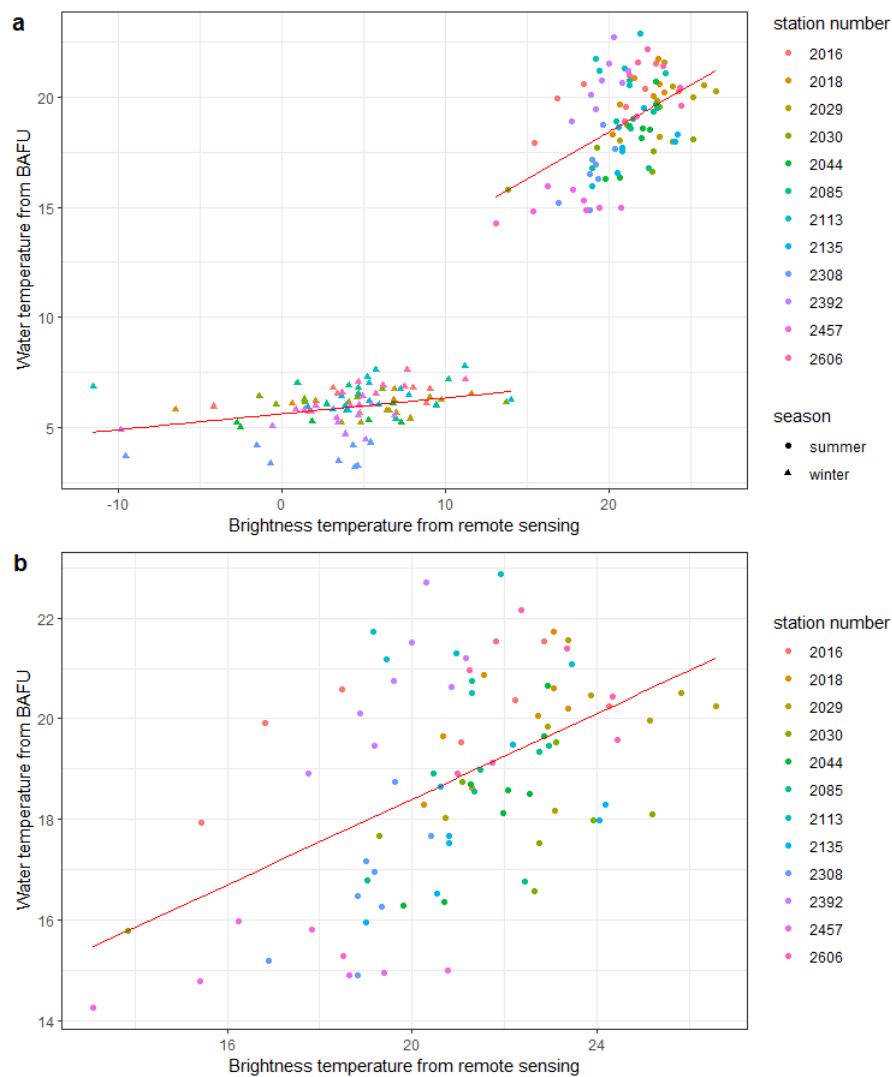


Figure 6 Linear model for brightness temperature extracted from remote sensing and water temperature measured by BAFU.

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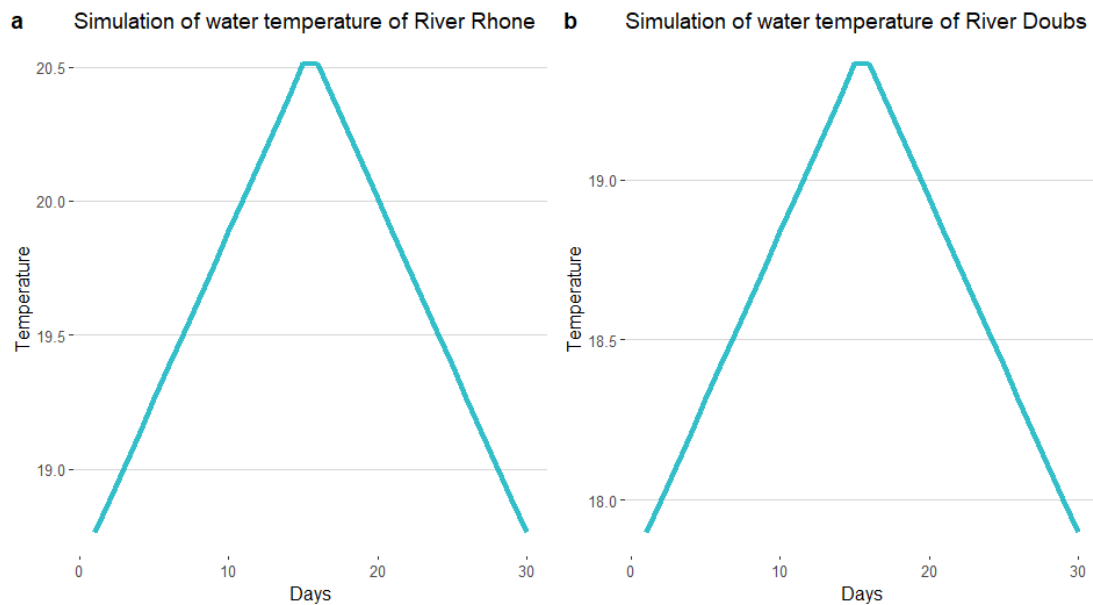


Figure 7 Simulation of water temperature in River Rhone (a) and River Doubs (b)

Three fish species (Burbot, Lake trout, Northern Pike) that are sensitive to high water temperature (with low CT_{max}) are selected to test our physiological model. Although the maximum temperature in summer 2018 was 19.19°C in River Doubs and 20.34°C in River Rhone, the upper thermal limits for all fish were not crossed for any single day in the simulation, as the lowest CT_{max} among all the fish species in our compiled data was 27.4°C for lake trout. Therefore, our physiological model showed zero effect of the 2018 heatwave on fish fitness.

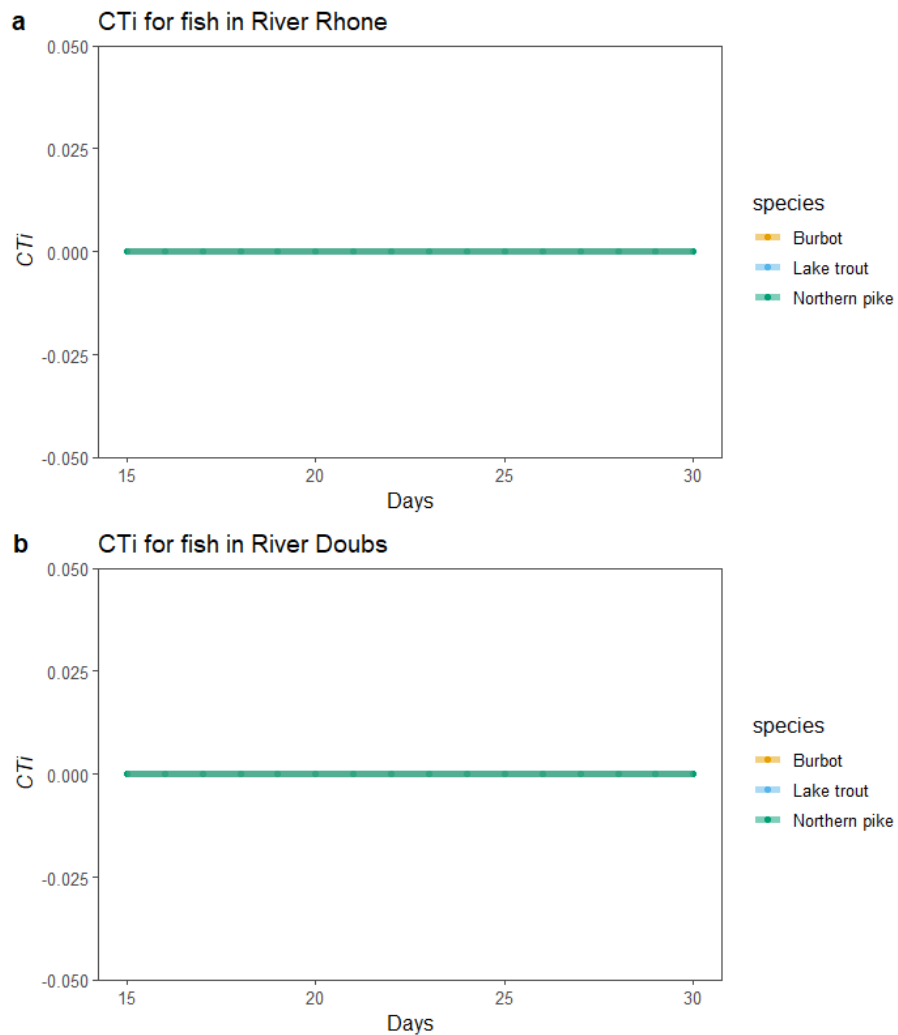


Figure 8 Critical temperature index for fish species in segments of River Rhone (a) and River Doubs (b).

Discussion

The physiological model for fish species has produced surprising results. While fish deaths were observed during the 2018 European Heatwave (BBC, 2018), our model indicated no effect of hot weather on fish survival in Switzerland. The inconsistency stems primarily from the limited amount of information we can gather from remote sensing data. The Landsat 8 satellite scans Switzerland every 16 days, meaning that we only have six sets of images for the entire summer (from July to September). Furthermore, image quality is highly dependent on

cloud cover and shadows. We are unable to obtain a time series of water temperature throughout the day, which fluctuates due to solar radiation and heat transfer from the atmosphere. As a result, the images we used to calculate water temperature were all taken at midnight or in the morning, when temperatures are cooler. Thus, the maximum temperature of 19.19°C in River Doubs and 20.34°C in River Rhone may not reflect the true situation, and fish could be suffering. A more accurate water temperature prediction model is expected from Konrad Bogner's group later this year, which will improve our physiological model's performance in aquatic ecosystems.

Fish deaths during European heatwaves are not solely caused by high water temperature. Fish rely on oxygen to survive, and warm temperatures can lead to very low dissolved oxygen levels (Sander, 1999). Extreme heat can also result in algal blooms, exacerbating the situation and making it difficult for fish to breathe. To better understand the physiological response of fish to heatwaves, it would be helpful for our model to incorporate dissolved oxygen levels.

Extreme weather has a significant impact on livestock health (Vitali et al., 2015). An increase in THI during summer can cause thermal discomfort in livestock species, affecting their performance and survival (Morignat et al., 2014). Our results show that high temperatures in Switzerland do cause stress in livestock, but it is not significant, particularly for cattle and sows. To improve our physiological model's accuracy in reflecting the real situation, we need to communicate more with local stakeholders and learn how milk production and other health conditions of livestock change during heatwaves in Switzerland. This information can help us adjust the thresholds of P_k and develop a model that better approximates the real situation.

It is worth noting that most previous research on the effects of heatwaves on livestock has focused on dairy cows. Our results show that horses are more sensitive to high temperatures and humidity. Therefore, farmers should prepare cooling measures for their horses before the heatwave arrives. Extreme weather also affects large mammals, and we must be cautious about the threat they pose to crops, domesticated animals, and people's safety as they migrate from their original habitats due to high temperatures.

High temperature is not the only threat to Swiss biota during heatwaves; it often co-occurs with water scarcity. Switzerland has experienced severe droughts during heatwaves, and in

worse conditions, the Swiss Army has had to airlift water to high mountain pastures to rescue cows from thirst (Mantovani, 2018). Unfortunately, our physiological model fails to capture and predict hydrological conditions in Switzerland. To address this limitation, we should consider collaborating with other groups in Malefix to incorporate drought and physiological stress into our final output of the risk index map.

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