Feeling the Heat

Franken, O.

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Summary

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With ongoing climate change, there is an increase in frequency, intensity and duration of extreme climatic events. This increase in extreme climatic events is ecologically very important as events, such as heat waves, can occur without prior warning and are more likely to surpass physiological thresholds of organisms. Therefore, these events can lead to altered species performance, species interactions, community composition and ecosystem functioning as a whole. Understanding, and possibly predicting, how ecological communities will be affected by extreme events is amongst the most pressing questions in ecological research. In this thesis I investigated how we can improve our understanding of the effects of extreme climatic events on communities of soil arthropods. One of the main difficulties in generalizing the effects of extreme events is due to the tremendous diversity of species in ecological communities. These different species can differ in their tolerance to extreme abiotic conditions, and therefore responses of species are not uniform. To overcome this, I applied a trait-based approach, in which a relevant trait (the Critical Thermal maximum) was measured which gives an indication of the sensitivity to a specific stressor (high temperature). I then used this trait in methods ranging from field and laboratory manipulations to a modelling approach, in order to gain a better understanding of the effects of extreme climatic events on soil arthropod communities.

In chapter 2, we tested whether we can directly compare the effects of different types of extreme climatic events, such as heat waves, cold spells, droughts, heavy precipitation and inundation with sea water. This study was also used to test which abiotic factors would have the strongest influence on community composition. To do so, we sampled the green beach of the Dutch barrier island Schiermonnikoog every six weeks for more than two years on two locations and in three vegetation types. Soil fauna was extracted from the samples and identified and counted under a binocular. The resulting data set of the soil arthropod community was then linked to environmental data from a nearby meteorological station to test if the composition of the community from one sampling point to the next would differ more if an extreme event took place in that period, compared to periods when no extreme events were recorded. While we did not find this pattern, we agre that this method of directly comparing the effects of different types of extreme events is very useful in generalizing how extreme events are affecting communities. Therefore, we strongly encourage other researchers with long-term ecological datasets to apply the same method to directly compare different types of extreme events. A major finding in this study was that especially temperature was linked to changes in community composition. Because of this finding, the next chapters of this thesis are focussed on temperature, specifically heat waves.

Chapter 3 describes a field manipulation experiment, where plots were heated on the green beach of Schiermonnikook to mimic heat waves. After the heating period, animals of the most dominant taxa were collected from both treatment and control plots to measure their Critical Thermal maximum (CT_{max}) at the individual level. The heating treatments did not induce an increase in thermal tolerance of species in the heated plots which could have been the result of both phenotypic plasticity and natural selection. However, we observed a considerable amount of variation in thermal tolerance within the species (i.e. intraspecific variation) and large differences in tolerance between different species (i.e. interspecific variation). Especially the most dominant prey species (*Isotoma riparia*, a springtail) had a much lower thermal tolerance compared to its most dominant predators, spiders from the families Linyphiidae (dwarfspiders) and Lycosidae (wolfspiders). This difference in tolerance can therefore lead to changes in community composition and altered species interactions when communities are exposed to extreme climatic events.

The observed difference in thermal tolerance between the interacting species led to another experiment in chapter 4, where we tested if the measured differences in CT_{max} could be linked to altered species performance, and if these differences would subsequently alter species interactions when the system was exposed to heat waves. To do so, we removed all animals from intact soil samples taken from our field site and reintroduced four different species combinations in these samples. In all samples the prey species *I. riparia* was present with either no predators, a Linyphiidae spider, a Lycosidae spider (*Pardosa purbeckensis*) or both these predators. These different species combinations were then divided over three heat wave treatments: no heat wave, i.e. 15°C during both day and night, a moderate heat wave with daily temperatures of 25°C and night temperatures of 15°C or extreme heat waves with day temperatures of 35°C and 15°C at night. We found that *I. riparia*, the species with the lowest thermal tolerance, was indeed most strongly affected by the high temperature, affecting both its survival and growth rate. The opposite pattern was observed for the Lycosidae predator, as their growth rate increased when exposed to the highest temperature treatments. We had hypothesized that there coula be an interaction between predator presence and heat wave treatment on the survival of *I. riparia*. Especially when considering that *P. purbeckensis* showed an increase in growth rate even despite the higher metabolic rate ectotherms face with high temperature, in combination with the already increased mortality caused by abiotic stress in *I. riparia*. However, instead of an interaction, we observed an additive effect which may indicate that the predators seek out the already weakened individuals of the prey population.

While field and laboratory experiments can provide strong empirical data on how extreme temperatures can influence the fate of species and interactions between species, it is very challenging to use empirical research to disentangle the different features of a heat wave. The intrinsically correlated nature of frequency, intensity and duration of climatic events makes it a challenge to experimentally separate them, especially when choices need to be made due to limitations of time, space and equipment. Therefore, in chapter 5, we applied a modelling approach using the individual-based model WEAVER to test which features (i.e. frequency of intensity) of a heat wave are most important in determining the effects of the extreme event. We created *in silico* experiments where the taxa that were studied in chapter 4 were exposed to combinations of eight temperature intensities and four heat wave frequencies, i.e. 32 treatments in total. We found evidence that in these simulations heat wave intensity is far more important than heat wave frequency when looking at species performance. Only when the intensity of the heat wave was affecting the range of intraspecific variation in thermal tolerance that was mentioned before, i.e. when only a part of the population is affected, exposure to a subsequent heat wave had additional effects on species performance. As shown in this study, using individual-based modelling approaches can be a powerful tool to gain a more mechanistic understanding of observed biological patterns. Moreover, such models can be used to generate new hypotheses and provide an indication of which treatments would be interesting to use in empirical tests.

When performing the experiments that form the basis of this thesis, it became apparent that the facilities that are commonly available to researchers, such as microcosms and climate rooms, would not be sufficient to create more complex and realistic climatic scenarios. Therefore, we developed the novel experimental setup CLIMECS (CLImatic Manipulation of ECosystem Samples), which is described in chapter 6. In this setup, intact soil cores collected from the field (i.e. including all microorganisms, plants and arthropods), can be exposed to very specific climatic scenarios in which both temperature profiles as well as precipitation events can be programmed, allowing for multi-stressor experiments. Moreover, the range of abiotic conditions that can be achived in this setup is much larger than in conventional manipulation systems, which allows the user to test abiotic conditions in the range of climatic extreme events. All the variation in abiotic variables that are induced by the treatments are automatically logged and plotted into graphs, allowing for easy monitoring of the experiments, and therefore less disturbance of the experimental units which makes it possible to keep experiments running for longer periods. Combined, the CLIMECS system allows researchers to test a whole new set of hypotheses, which will greatly add towards our understanding of our rapidly changing natural world and might even allow us to anticipate on the changes to come.

In the synthesis of this thesis, chapter 7, I place the main findings of the different chapters into a wider context. In general, I conclude that: i) By using datasets which combine community composition over time and environmental data, it is possible to directly compare the effects of different types of extreme climatic events. ii) The use of ecophysiological traits is a valuable tool to indicate species tolerance to adverse abiotic conditions, especially when the traits directly link to the abiotic factor that is being investigated. iii) The intraspecific differences in ecophysiological traits may function as an ecological rescue mechanism if the more tolerant individuals survive the period of abiotic stress. iv) Individual-based models are a useful tool to gain a more mechanistic understanding of observed patterns in nature and are very useful to generate new hypotheses that can be tested in either the field or under laboratory conditions, or to focus research effort to the most promising manipulations. And, v) That novel experimental setups such as our CLIMECS setup can facilitate testing of hypotheses which were previously either impossible or unfeasible to perform. Ultimately, I argue that large-scale collaborations between research groups could facilitate answering big ecological questions such as how the effects of climate change are affecting natural ecosystems, and how ecosystems respond to the expected changes. These questions urgently need an answer in the context of rapid climate change and ongoing intensification of anthropogenic influences on natural systems. Hopefully the developed methods and obtained results in this thesis will help to bring us one step closer to finding these answers.