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Increasing temperature and decreasing specific leaf area amplify centipede predation impact on Collembola

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ABSTRACT

Collembola is an abundant group of soil organisms playing a major role on litter decomposition process and nutrient cycling in forest ecosystems. Habitat structure strongly influences Collembola assemblages as plant litter physical characteristics and quantity provide structural niches and determine the outcome of their interactions with predators. Collembola are also extremely sensitive to environmental conditions such as soil temperature that control their demographic parameters and activity. In this context, increasing temperature with the ongoing climate change can have strong impact on Collembola assemblages and their responses to predation either directly by altering their behaviour or indirectly by altering their habitat structure. We therefore examined how the increase of temperature combined to the decrease of specific leaf area (SLA, a major functional plant trait) of the European common oak (*Quercus robur* L.) and the presence of a centipede predator (Chilopoda: Lithobiidae) will affect the abundance of *Folsomia candida* (Collembola: Isotomidae) in a 5-week microcosm experiment. Increasing temperature, decreasing SLA and presence of centipede altered *F. candida* abundance. We observed a significant temperature × predation interaction suggesting differential effects of increasing temperature on *F. candida* abundance with and without predator. We also observed a significant SLA × predation interaction highlighting that lower SLA decreases *F. candida* abundance only in predator presence. Finally, our findings evidenced that increasing temperature and decreasing SLA amplify the negative effect of centipede predation on *F. candida* abundance, suggesting that both direct and indirect effects of climate change would conjointly strengthen the top-down control of predators on preys.

1. Introduction

Soil biodiversity plays an essential role in ecosystem functioning, especially in biogeochemical cycles [1,2] with feedback on plant growth, ecosystem productivity and overall community structure [3,4]. It has become increasingly clear during the last decades that soil biodiversity and related ecosystem services are extremely threatened by climate change [5,6], through changes in species demographic parameters, species interactions [7,8], and eventually cascading effects on ecosystem processes [9,10]. As predator-prey interactions are a key structuring force in population dynamics [11,12], understanding the effects of climate change on these interactions is of primary importance to predict soil ecosystem responses.

Collembola, among the most widespread and abundant group of soil organisms [13], plays a major role in soil functioning [14] by regulating the microbial (bacterial and fungal) communities, litter decomposition process and nutrient cycling, and consequently feedback on plants [15–18]. Collembola are also strongly top-down controlled by many predators including spiders [18,19], centipedes [20,21] or mites [22,23]. Furthermore, Collembola are often under the influence of habitat structure as plant litter physical characteristics and quantity (i.e. litter thickness) provide niches serving as microhabitats for Collembola [9,19,21,24]. This habitat structure also acts as an important driver of prey-predator interactions by influencing encounter probabilities between Collembola and their predators [19,21].

As Collembola are also extremely sensitive to environmental conditions [13], increasing temperature and decreasing precipitation induced by ongoing climate change [25–27] can have strong direct

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impacts on Collembola demographic parameters (e.g. reproduction, development and survival) by altering both soil temperature and moisture conditions [28–30]. As ectothermic organisms, Collembola and their predators generally exhibit greater activity with warming because of elevated metabolic demands [31]. Several experimental field studies, simulating the impact of future climatic conditions in grassland and forest ecosystems, reported a decline in Collembola abundance and diversity in warmer and drier soil conditions, whereas they increased in warmer and wetter soils [9,30,32–34]. While there is a recent wealth of literature on warming effect on prey-predator interactions [26,35–37], few attempts have been made on belowground organisms. For example Thakur et al. [23] reported that predatory mites (*Hypoaspis aculeifer* and *H. miles*) reduced Collembola coexistence (*Folsomia candida* and *Proisotoma minuta*) with increasing temperature.

In addition, the ongoing climate change can also indirectly affect Collembola by altering litter physical characteristics and quantity produced by plants with thus cascading effects on both the food resource and microhabitat availability for Collembola as well as the outcome of their interactions with predators. In fact, climatic conditions strongly control leaf traits and consequently induce changes in litter traits [38–40]. Plants under warmer and drier climates tend to have thicker leaves (i.e. sclerophylly) and lower specific leaf area (SLA) in order to reduce water loss [40,41]. For example, Graça and Poquet [42] reported that SLA of *Quercus robur* and *Alnus glutinosa* leaves decreased with increasing temperature across a wide European climatic gradient. As a consequence, for hemi- and epedaphic Collembola (i.e. living on the soil surface and in the leaf litter), this decrease in SLA could imply (i) a lower surface area for fungal colonization leading to a reduced fungal grazing, as well as (ii) less spatial refuges and higher probability to encounter their predators. However, to our knowledge, no previous study attempted to evaluate the consequences of a decrease in SLA on Collembola populations and their interactions with predators.

Thus, our current understanding of soil organisms' responses to climate change drivers is still limited by a lack of studies addressing conjointly both direct and indirect effects of climate change on these organisms and their interactions. To address this gap, we designed a full factorial experiment in order to evaluate how the increase of atmospheric temperature (15 °C, 20 °C and 25 °C), the decrease of SLA (15.9 ± 0.5 *vs.* 11.7 ± 0.3 $mm^2 mg^{-1}$) of European oak leaves (*Quercus robur* L.) and the presence or absence of a centipede predator (Chilopoda: Lithobiidae) affect the abundance of *Folsomia candida* (Collembola: Isotomidae) in a 5-week microcosm experiment. The elevated temperature treatments were established in order to represent moderate (+5 °C) to high (+10 °C) climate warming scenarios [27], whereas the lowest temperature treatment was based on the climate at which *F. candida* was thermally acclimated (i.e. 15 °C). The decrease of SLA was established to simulate the impact of lower surface area for a same litter mass leading to an alteration of habitat structure. Previous to the experimentation, we carefully checked that the two oak litters (high and low SLA) only differed in their physical traits and not on their chemical traits (i.e. C:N ratio and phenolic concentration). We hypothesized that increasing temperature would induce higher predation effects on *F. candida*, as both prey and predator become more active and must encounter each other more frequently. We also hypothesized that decreased SLA would induce higher predation effects on *F. candida*, as a decrease in habitat complexity provides less spatial refuges for the prey population. Finally, the combination of both direct (i.e. temperature) and indirect (i.e. habitat structure) effects of climate change would conjointly strengthen the top-down control of predator on *F. candida*.

2. Materials and methods

2.1. Material collection

2.1.1. Leaf litter

The experiment was conducted using leaf litter of a common and widespread deciduous tree in temperate European forest: the European oak (*Quercus robur* L.). Freshly-abscised shade leaves were collected on 5 individuals during the litter fall period (autumn 2016) in the Paimpont Forest (48°01′N, 2°10′W) and in the Rennes Forest (48°11′N, 1°34′W), northwestern France. In February 2017, 200 g of the leaf litter from both forests were enclosed in 0.5-mm mesh size litterbags and put on the litter layer under oak trees of the University of Rennes 1 campus (48°07′N, 1°38′W) in order to allow litter microbial colonization. Litter samples were collected after 2 months, dried at 40 °C for 48 h and frozen at −18 °C for 48 h in order to remove animals, and then stored in a dark room at ambient temperature until the start of the experiment.

Ten leaves were used to determine the specific leaf area (SLA) of *Q. robur* leaves for each forest. SLA was calculated as the ratio between leaf area and leaf dry weight and determined by weighing (± 0.01 mg) 3 leaf disks obtained with a cork borer (10 mm diameter) from the 10 randomly chosen leaves [42]. The leaf dry weight was determined after drying leaf samples at 60 °C for 48 h. Oak leaves of Paimpont Forest showed a mean SLA of 15.9 ± 0.5 $mm^2 mg^{-1}$ (thereafter high SLA) while those of Rennes Forest showed a significant 26% lower SLA with a mean of 11.7 ± 0.3 $mm^2 mg^{-1}$ (thereafter low SLA) (*t*-test = 7.0, $P < 0.001$). In addition to SLA, C:N ratio and phenolic concentration of the two litter types were measured as these two plant functional traits were reported to also influence Collembola population dynamics [9,24,43]. Carbon and N concentrations were determined by thermal combustion using a CN analyzer. Phenolic concentration was measured colorimetrically using the method described in Santonja et al. [44] with gallic acid as a standard. Leaf litter types of high and low SLA showed no significant difference in both C:N ratio (37.6 ± 0.6 *vs.* 40.6 ± 1.1, respectively; *t*-test = −2.3, $P = 0.063$) and phenolic concentration (49.3 ± 0.8 *vs.* 51.8 ± 0.9 $mg\,g^{-1}$, respectively; *t*-test = −1.8, $P = 0.123$). As our research hypothesis was based on a physical effect of *Quercus* litter on predator-prey interaction (i.e. habitat structure) and not on a chemical effect of this litter (i.e. trophic or toxic role), we considered that we used two litter types exhibiting similar chemical properties but distinct physical properties to perform our experiment.

2.1.2. Collembola and centipede

The experiment was conducted using two well-represented invertebrate groups from the leaf litter of European oak (*Quercus robur* L.) forests: Collembola as the prey and Chilopoda as the predator. Collembola used in this experiment was *Folsomia candida* (Collembola: Isotomidae), a parthenogenetic and ubiquitous hemiedaphic species known as fungivorous and frequently used in laboratory experiment [23,45]. Individuals were reared in plastic boxes (5.5 cm diameter × 7 cm height) containing a flat mixture of plaster of Paris and activated charcoal in a ratio 9:1, permanently water saturated. Individuals had been cultured at 15 °C and fed *ad libitum* with dry yeast pellets. To synchronize the age of the organisms, oviposition was stimulated by placing adults on a new breeding substrate [45]. After oviposition, adults were removed and the eggs hatched 3–4 days later. To ensure that the population was as homogeneous as possible, eggs were placed in a large container and juveniles were fed for the first time altogether. We used 10–12 days juveniles of similar size (0.90 ± 0.08 mm; n = 10) that were starved 48 h before the start of the experiment.

Lithobiid centipedes (Chilopoda: Lithobiidae) were used as predator in this experiment. They are known as active predators that live in the upper soil layers pursuing prey such as Collembola [13,46]. The centipedes were manually collected by sifting oak leaf litter of the Paimpont Forest. After collection, collected centipede individuals of similar size (10.81 ± 0.65 mm; n = 10) were kept separate from each other in moistened plastic boxes at 15 °C and were fed *ad libitum* with *F. candida* individuals. Centipede individuals were also starved 48 h before the start of the experiment.