

## How will climate change affect the feeding biology of Collembola?

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### ABSTRACT

Collembolans are one of the most diverse and abundant group of soil invertebrates. Recent studies have shown anthropogenic climate warming to alter Collembola diversity and density in warm-dry (more detrimental effects) and warm-wet (lesser detrimental effects) conditions. Besides the direct influence of abiotic stressors, shifts in food availability could help understand variable collembolan responses to climate warming. Collembolan diet is generally formed by two main groups of soil fungi: saprotrophic and mycorrhizal fungi, which occupy different spatial niches in the soil, and are simultaneously affected by climate warming and drought. These fungal responses to climate change alter food availability for Collembola, inducing shifts in their dietary composition. Collembolans preferentially consume saprotrophic fungi, regardless of their spatial niche. However, those inhabiting deeper soil layers occasionally feed on mycorrhizal fungi and rely more frequently on such diets when other food sources become scarce. We suggest that climate change-driven scarcity of saprotrophic fungal diets in soils would make collembolans depend more on mycorrhizal fungal diets. We then discuss how such dietary shifts are driven by distinct mechanisms in warm-dry and warm-wet soil conditions. We finally call for the use of emerging techniques (e.g., stable isotope analysis, molecular gut content) to quantify the diets of Collembola more accurately under different climate change scenarios, which will help us shed more insights on how warming and precipitation variability are going to alter Collembola-fungal trophic interactions in a changing world.

### 1. Current understanding of Collembola feeding biology

Collembolans (or springtails) are one of the most diverse groups of soil invertebrates (Rusek, 1998; Petersen, 2002; Coleman et al., 2018; Potapov et al., 2022). The feeding biology of Collembola has been a major research area in soil ecology given their vast range of microbial and plant-based diets (Chahartaghi et al., 2005; Ruess et al., 2007; Potapov et al., 2016a). Their feeding activities have important consequences on the decomposition of organic matter, soil nutrient dynamics and plant performance (Peguero et al., 2019; Rusek, 1998; Eisenhauer et al., 2011; Jernigan et al., 2022). Recent studies using isotopic signatures of Collembola diets have revealed soil fungi as their major food source, predominantly saprotrophic fungi (Fujii et al., 2021; Li et al., 2022) (Fig. 1, see Box 1). Yet, the importance of mycorrhiza as a food source of Collembola has been often contested (Potapov & Tiunov, 2016; Pollierer and Scheu, 2021), since some mycorrhizal fungi contain deterrent compounds that may be remarkably efficient against microarthropod feeding (Duhamel et al., 2013), while other mycorrhizal fungi

are only accessible in deeper soil layers (Caravaca and Ruess, 2014; Anslan et al., 2016). Furthermore, within mycorrhizal groups, feeding on arbuscular mycorrhizal fungi (AMF) is preferred compared to ectomycorrhizal fungi (EMF), given that feeding on EMF requires higher specialization (e.g., sucking on hyphal cytoplasm in the case of Protura; see Bluhm et al., 2019; Galli et al., 2019). Climate change can alter resource availability for collembolans (Blankinship et al., 2011; Jansson and Hofmöckel, 2020). This leads to shifts in fungal feeding through behavioural diet switching and/or changes in collembolan community composition (Anslan et al., 2018; Potapov et al., 2021). Here, using recent advances in our understanding of mixed fungal diets of Collembola, we propose how climate change-induced shifts in fungal resource availability are going to alter the feeding biology of Collembola. To this end, we discuss various scenarios through which Collembola-fungal feeding interactions will change with saprotrophic and mycorrhizal fungi in warm-wet and warm-dry soil conditions. We acknowledge that dietary shifts towards food resources other than fungi, such as bacteria or fine roots, should also be taken into consideration (Potapov et al.,

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2021). However, climate-induced shifts within fungal groups are more relevant for Collembola given that other food items might become similarly limited due to climate change (Blankinship et al., 2011; Jansson and Hofmockel, 2020) and because most Collembola have predominantly morphological and biochemical adaptations to feed on fungi (Potapov et al., 2021).

## 2. Collembola responses to climate change

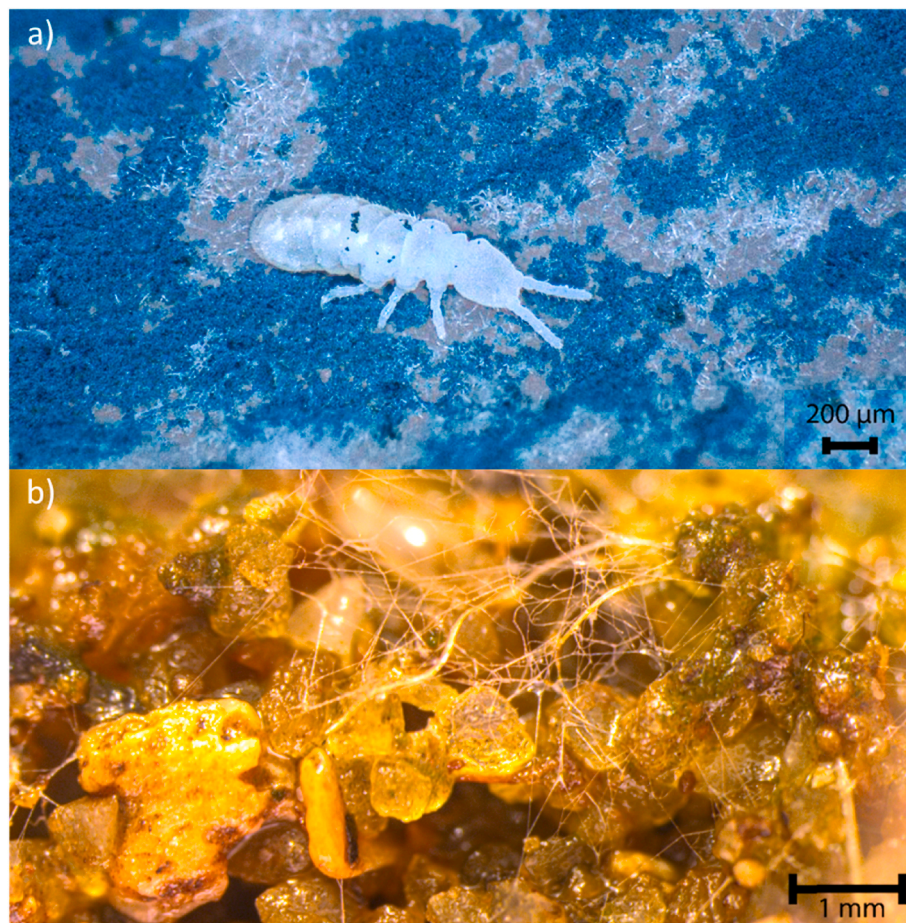
Climate change negatively impacts collembolan abundance and its feeding activities mostly in drier soil conditions (Blankinship et al., 2011; Wang et al., 2022), directly caused by more frequent and long-lasting droughts (Peguero et al., 2019), or indirectly through enhanced evapotranspiration at higher temperatures (Kardol et al., 2011; Vestergård et al., 2015). By contrast, moderate warming (e.g., temperature within thermal optimum of collembolans) exerts neutral (Peng et al., 2022; Holmstrup et al., 2013; Peguero et al., 2019, Turnbull and Lindo, 2015) or even positive effects on Collembola (Chauvat and Forey, 2021) when resources are sufficiently available along with favourable moisture (Thakur, 2020; Meehan et al., 2020), most likely because warming induces higher metabolic rates and enhances their biological activity (Ehnes et al., 2011; Gillooly et al., 2001).

The spatial niche of Collembola across the soil profile provides important insights into how they could respond to warming and drought. For instance, surface-dwelling epedaphic species are considered more tolerant to warm and dry conditions than sub-surface living hemi-edaphic and deep-soil living euedaphic ones (Salmon et al., 2014; Ferrín et al., 2023; Thakur et al., 2023). In turn, deep-soil living

collembolans experience a less variable abiotic environment and are thus more susceptible to temperature and water variability caused by warming and precipitation extremes (Makkonen et al., 2011; van Dooremalen et al., 2013; Thakur et al., 2023). Besides, epedaphic species have greater dispersal abilities (Ponge, 2020) allowing them to potentially escape horizontally (as opposed to vertical dispersal to deeper soil layers, which is more common in hemi- and euedaphic species) to track more benign microhabitats during harsh conditions (Salmon et al., 2014; Ferrín et al., 2023). This could explain the apparent edaphisation (i.e., increased representation of hemi- and euedaphic species) of collembolan communities in field experiments simulating warmer and drier climatic conditions, since epedaphic Collembola can escape more easily from unsuitable abiotic conditions (Ferrín et al., 2023, Holmstrup et al., 2013; Yin et al., 2019; Krab et al., 2013).

## 3. How will climate change alter Collembola-saprotrophic fungi-mycorrhizal fungi interactions?

Given the temperature-dependence of metabolism and the fact that thermoregulation in ectotherms is limited, the pace of most biological processes (e.g., feeding and/or moving) in Collembola will accelerate due to warming (Brown et al., 2004; Kutcherov et al., 2020; Ott et al., 2012). We argue that this will drive Collembola to rely more often on their secondary food sources, such as mycorrhizal fungi. More specifically, higher energetic demands of collembolans could intensify their foraging rates and force them to move at further distances where their primary food sources, such as saprotrophic fungi, may not always be readily available (Englund et al., 2011). Reduced precipitation, in turn,



**Fig. 1.** a) An euedaphic collembolan (*Protaphorura macfadyeni*) feeding on a saprotrophic fungus (*Trichoderma asperellum*); b) Extraradical mycelium (ERM) of an arbuscular mycorrhizal fungus (AMF; *Rhizophagus irregularis*) growing on mineral substrate.

is likely to decrease the availability of saprotrophic diets and further constrain high collembolan abundances mainly to moist spots in the soil (e.g., deeper soil layers), thereby altering their spatial distribution and forcing dietary shifts to secondary food sources. Indeed, such dietary shifts will vary among three major ecological groups of Collembola (epedaphic, hemiedaphic, euedaphic; Glossary), and more importantly, how saprotrophic and mycorrhizal fungi respond to climate warming under wet or dry conditions (see Box 2 for more information). To this end, we discuss how collembolan-saprotrophic and collembolan-mycorrhizal fungal interactions change in warm-wet and warm-dry soil conditions to highlight several scenarios of shifts in collembolan feeding biology in a changing world (illustrated in Fig. 2). We further outline the causes of such feeding shifts and their consequences for ecosystem functioning. We consider warm-wet conditions as increased temperature and soil moisture due to higher precipitation, as one of the predicted future scenarios of anthropogenic climate change in many boreal and (sub-) tropical regions (IPCC 2023). In turn, warm-dry conditions represent increased temperature and decreased soil moisture due to reduced precipitation, which are likely to occur in several temperate and semi-arid regions, as well as in the Amazon basin (IPCC 2023).

### 3.1. Collembola-saprotrophic fungal feeding interactions (warm-wet conditions)

Warm and wet conditions are mostly favourable for the growth of litter- and soil-dwelling saprotrophic fungi. However, this positive effect can get overturned as carbon substrates become more limiting, particularly with long-term warming (Pec et al., 2021). As a result, declines in carbon-rich substrates will reduce the availability of saprotrophic fungi over prolonged periods (Feng et al., 2022).

Diet switching following a shortage of saprotrophic fungi is likely and detrimental for Collembola species depending on litter-derived food sources, mainly epedaphic and hemiedaphic Collembola (Caravaca and Ruess, 2014; Kühn and Ruess, 2021). Epedaphic species are capable of

switching to other resources available close to the soil surface (e.g., lichens, algae; Potapov et al., 2021), whereas hemiedaphic species will be forced to move deeper in the soil to feed more on root-derived food sources (i.e., mycorrhizal and root-associated saprotrophic fungi; Potapov et al., 2016a; Potapov et al., 2016b; Li et al., 2022). Yet, certain groups of saprotrophic fungi will sporadically grow in abundance in warm-wet conditions shortly after litter deposition (Feng et al., 2022), creating pulses of food availability for Collembola species heavily relying on them and allowing their persistence (Potapov et al., 2023). Euedaphic collembolans mostly rely on root-derived food sources (Potapov et al., 2021), so they could be less affected by the shortage of litter-derived saprotrophic fungi. Still, they are expected to switch more often to mycorrhizal diets to fulfil their higher metabolic demands driven by warming, given that these food sources generally remain available in warm and wet conditions.

Changes in Collembola feeding in colder areas could be further clarified by investigating areas currently experiencing warm conditions using space-for-time substitution. For instance, tropical regions, characterized by warm and wet conditions with fast litter turnover, usually harbour Collembola communities with lower abundances but similar species richness compared to those from temperate and cold regions (Potapov et al., 2023). Food sources for collembolans are thus limited in tropical regions, probably as a result of the lower availability of saprotrophic fungi (Feng et al., 2022). Further research on the main feeding strategies of collembolans in tropical areas could provide important insights to predict potential diet shifts in other biomes that will experience warmer and wetter conditions due to climate change.

We suggest that increased limitation of soil C sources under warmer and wet conditions will generally reduce the abundance of litter-derived saprotrophic fungi and therefore its availability as a food source for Collembola, which will be subsequently forced to rely more often on secondary food resources. This feeding shift will have an overall negative impact on collembolan densities, but those species strongly depending on litter-derived saprotrophic diets could manage to track saprotrophic fungi growing after occasional fresh litter inputs.

#### Box 1

##### Collembola-fungal feeding interactions

Saprotrophic fungi are the most preferred diet of Collembola. This preference has been confirmed through several feeding choice experiments, such as when Collembola are given the choice among various food items (e.g., fungal, bacterial or algal), they mostly prefer saprotrophic fungi with a concomitant increase in their fitness (Table 1). Moreover, they often exhibit selective feeding on certain fungi even among their preferred saprotrophic fungal diets (Jørgensen et al., 2005), which might explain resource partitioning in Collembola species living in similar soil depths (Jørgensen et al., 2003). Top-down regulation of Collembola on saprotrophic fungi is generally weak (A'Bear et al., 2014b; Lang et al., 2014), potentially due to the several fungal defences against mycelia consumption, including repellent metabolites (Scheu and Simmerling, 2004) and crystalline structures (Böllmann et al., 2010). However, by displaying distinct feeding preferences, Collembola could influence interactions among saprotrophic fungal species, such as by restricting competitively superior species through apparent competition (Crowther et al., 2011; A'Bear et al., 2013; Thakur and Geisen, 2019). Moreover, collembolan grazing on saprotrophic fungi influences decomposition of soil organic matter (Rusek, 1998; Tiunov and Scheu, 2005). Numerous studies have reported on the negative effects of collembolan feeding on saprotrophic hyphal extension (A'Bear et al., 2012; Crowther et al., 2013), which exaggerate the competitive superiority of mycorrhizal fungi over saprotrophic fungi for space and resources (Bödeker et al., 2016; Thakur et al., 2019). For example, Tiunov and Scheu (2005) found that the presence of mycorrhizal fungi decreased the abundance of numerous saprotrophic species driving a significant shift in saprotrophic community structure. This shift was exacerbated in the presence of Collembola, which is thought to destabilise saprotrophic fungal communities making them more susceptible to the influence of mycorrhizal fungi.

Severe collembolan grazing on the hyphae of mycorrhizal fungi can impair transportation of nutrients through mycorrhiza to the host plant (Johnson et al., 2005). However, several studies have shown that moderate grazing by Collembola on the extra radical mycelium (ERM; Glossary) leads to higher mycorrhizal colonization of roots, and subsequent increase of nutrient sequestration in roots (Lussenhop, 1996; Gange, 2000; Ngosong et al., 2014). It is assumed that this effect is due to Collembola feeding on senescent hyphae, thereby releasing immobilized nutrients into the soil and benefitting mycorrhizal fungi and their host plants (Kaneda and Kaneko, 2004; Ngosong et al., 2014). Moreover, the feeding activity of Collembola on mycorrhizal spores facilitates the dispersal of mycorrhizal spores via defecation (Bakonyi et al., 2002; Seres et al., 2007). However, the effects of collembolan grazing on mycorrhizal fungi are density-dependent: low grazing intensity can be facilitative and high grazing intensity damaging to mycorrhizal fungi (Klironomos and Ursic, 1998; Bakonyi et al., 2002; Crowther et al., 2013; Steinaker and Wilson, 2008). A key challenge for several Collembola species is to access mycorrhizal fungi that occur deeper than many saprotrophic fungi in the soil (Lindahl et al., 2007; Anslan et al., 2016).



**Box 2****Fungal responses to warming and drought**

Saprotrophic fungi are crucial regulators of the turnover of terrestrial carbon and nutrient cycling (Feng et al., 2022), mainly by enabling the decomposition of highly abundant insoluble organic matter (Valášková et al., 2007) that can later be easily consumed by other organisms (Grinhut et al., 2007).

Several studies have shown that warming usually increases the biomass of these fungi (Semenova et al., 2015; Zhang et al., 2014; Treseder et al., 2016; Gang, 2019); however, some studies also report reduced biomass at higher temperatures (DeAngelis et al., 2015; Che et al., 2019). Indeed, the duration of warming exposure could be partly responsible for this lack of consistency in saprotrophic fungal responses to warming (Melillo et al., 2017). In a soil warming experiment (+5 °C above ambient temperature) running for more than 20 years (Melillo et al., 2017), the relative abundance of saprotrophic fungi remained unaltered after 5 years of warming but then decreased after 20 years with increased soil temperatures (Pec et al., 2021). Given that saprotrophic fungi are tightly associated with soil carbon sources (e.g., cellulose, lignin), the observed decline of saprotrophic fungi (DeAngelis et al., 2015), followed a warming-induced reduction of soil carbon content (Pec et al., 2021). Since warming enhances overall microbial activities, competition of saprotrophic fungi with other microorganisms for carbon substrates (e.g., bacteria, mycorrhizal fungi; Morrison et al., 2019) could constrain their growth under warmer conditions (Pec et al., 2021; but see Querejeta et al. (2021) for a case of enhanced competitive dominance of saprotrophic fungi in response to warming and drought).

Saprotrophic fungi generally suffer more from drought compared to warming (Boddy, 1999; A`Bear et al., 2014a). This is because resource acquisition for saprotrophic fungi is strongly limiting in dry soils, since solute diffusion (e.g., nutrients, extracellular enzymes) is disrupted at low soil moisture (Manzoni et al., 2012) and therefore constrains the breakdown of organic matter (A`Bear et al., 2014a). Cord-forming saprotrophic fungi are a particular exception to drought intolerance, as their ability to translocate water from moist substrates confers them with enhanced desiccation resistance (A`Bear et al., 2014a; Guhr et al., 2015).

Mycorrhizal fungi are one of the most dominant fungal groups in the soil, that usually form obligatory symbiotic relationships with several vascular plants. There is increasing evidence that warming effects on mycorrhizal fungi occur through shifts in the proportion of root length colonised (RLC) and extraradical mycorrhizal mycelium (ERM) in the soil (Rillig et al., 2002; Heinemeyer and Fitter, 2004; Staddon et al., 2004; Herzog et al., 2013; Yang et al., 2013). This effect could be attributed to the lengthening of the growing season and increased nutrient cycling (Piao et al., 2007), which thereby, enhances carbon allocation from host plants to mycorrhizal partners (Rillig et al., 2002; Mohan et al., 2014; Kim et al., 2015; Birgander et al., 2017). Warming may thus increase the abundance of mycorrhizal fungi to more responsive host plants (Bennett and Classen, 2020). Warming can further create more favourable conditions for mycorrhizal families with more competitive traits, such as edaphophilic species (Chagnon et al., 2013; Cao et al., 2020), which invest more biomass in extraradical hyphae than in root-borne structures, compared to rhizophilic species (Hart and Reader, 2002). As such, shifts in the abundance of different mycorrhizal taxa under warming may be linked to competitive capabilities. These competitive traits determine how well mycorrhizal fungi can accumulate nutrients in warm conditions with enhanced rates of soil N and P cycling processes such as mineralization and nitrification (Hart and Reader, 2002; Salazar et al., 2020; Xu et al., 2021).

Droughts have frequently been reported to reduce ERM (Augé, 2001; Staddon et al., 2003; Mohan et al., 2014; Weber et al., 2019; Hagenbo et al., 2021). This reduction of the mycelium could be attributed to a cutback in carbon supply obtained from the host plant; as droughts induce stomatal closure, which impedes plant's photosynthetic capacity and carbon supply belowground (Fuchslueger et al., 2014; Hasibeder et al., 2015). Furthermore, reductions in soil moisture can reduce the functioning of mycorrhizal hydrolytic enzymes, thereby inhibiting the breakdown of soil organic matter and nutrient acquisition (Herzog et al., 2013; Sardans and Peñuelas, 2013). Such declines in mycorrhizal functioning may prompt a shift in fungal community composition, supporting more drought tolerant species with a lower ERM biomass and with specific functional adaptations against drought stress (Gordon and Gehring, 2011; Gehring et al., 2014; Zhang et al., 2016). Such shifts have been observed between mycorrhizal groups with greater AMF dominance over EMF (Querejeta et al., 2009, 2021). Between arbuscular mycorrhizal families, studies have shown that drought-induced shifts in community composition are due to a relative increase in rhizophilic species over the edaphophilic ones (Allen et al., 1995; Chaudhary et al., 2014; Weber et al., 2019). This perceived intolerance of edaphophilic mycorrhizal species to arid environment could be accounted to their longer and finer ERM, which increases the surface area exposed to the surrounding soil matrix and make them more vulnerable to desiccation (Weber et al., 2019).

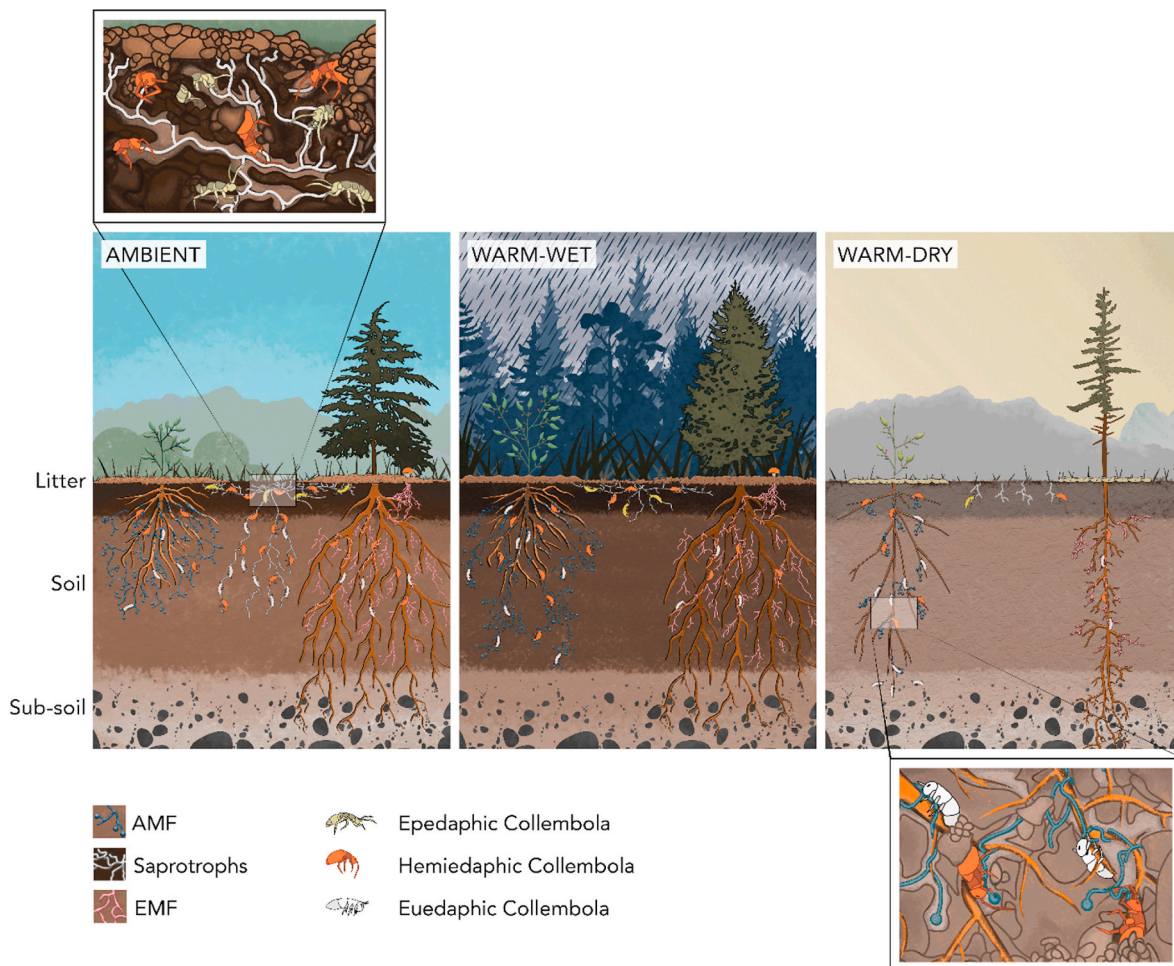
### 3.2. *Collembola*-mycorrhizal fungal feeding interactions (warm-wet conditions)

Enhanced growth and nutrient availability of the host plant in response to warming induce greater mycorrhizal biomass (Rillig et al., 2002; Mohan et al., 2014). This growth response of mycorrhizal fungi increases their competitive interactions with saprotrophic fungi and thereby reduces the preferred palatable substrate of *Collembola*, particularly for epedaphic species (Table 1; Gange, 2000; Tiunov and Scheu, 2005; Rohlf and Churchill, 2011).

Ectomycorrhizal fungi (EMF) typically form an extensive network of extraradical hyphae 2.5–6 times larger than that of arbuscular mycorrhizal fungi (AMF) per unit length of colonised root and are therefore highly present within the soil and available to *Collembola* (Olsson et al., 2003). However, EMF species possess antifeedant mechanisms, for example, through the production of calcium oxalate (Arocena et al., 2001). As such, opportunistic feeding on EMF may be limited to certain *Collembola* species adapted to overcome these defences (Böllmann

et al., 2010; Rohlf and Churchill, 2011), notably some euedaphic species (Zieger et al., 2017; Pollierer and Scheu, 2021). Although warming will accelerate the growth of mycorrhizal fungi, it may equally enhance the production of secondary metabolites, which further reduce their palatability for *Collembola* (LeFait et al., 2019).

Studies investigating AMF species responses to warming have shown more positive responses to warming for edaphophilic families (Gigasporaceae and Diversisporaceae) compared to rhizophilic AMF (Glomeraceae) (Cao et al., 2020; Xu et al., 2021). Moreover, collembolans tend to show higher affinity for grazing on edaphophilic AMF (Gigasporaceae) (Caravaca and Rues, 2014). This may, in part, be due to morphological differences where individuals from the family Gigasporaceae produce larger quantities of extraradical mycelium (ERM) with finer hyphae and are therefore more readily available to grazers (Hart and Reader, 2002). We, therefore, suggest that warming would increase the mycorrhizal presence and may shift mycorrhizal community composition to increase the accessible mycorrhizal fungi as a food source for *Collembola* (see Box 2).



**Fig. 2.** Climate-driven shifts in Collembola feeding on different functional groups of fungi (AMF, saprotrophs, EMF; see Glossary) depend on the prevailing soil moisture conditions and the vertical distribution of Collembola along the soil profile (epedaphic, hemiedaphic, euedaphic; see Glossary). The following soil layers are displayed, from top to bottom: litter (i.e., fallen leaves and fragmented debris), soil (i.e., varying in the content of organic matter, from higher content of organic matter in darker and shallower areas, to lower content in lighter and deeper areas), and sub-soil (i.e., mostly composed of mineral substrate). Three future climatic scenarios are represented in the main panels: ambient (i.e., current average temperature and moisture conditions), warm-wet (i.e., increased temperature and increased moisture due to high precipitation as one of the future scenarios of anthropogenic climate change) and warm-dry (i.e., increased temperature and decreased moisture due to reduced precipitation as one of the future scenarios of anthropogenic climate change). A detailed visualisation of Collembola feeding on fungi is displayed in the small panels. Note that reduced availability of saprotrophic fungi in warm-wet and warm-dry conditions prompts collembolans to feed more on mycorrhizal fungi, particularly AMF. This feeding shift is mostly driven by hemiedaphic and euedaphic collembolans, as they will enhance their activity in deeper soil layers to find food sources and, in the warm-dry scenario, to escape exceedingly dry conditions near the soil surface. This figure illustrates the proposed scenarios and suggested responses of all trophic groups based on the available evidence to date.

### 3.3. Collembola-saprotrophic fungal feeding interactions (warm-dry conditions)

Under warm and dry conditions, saprotrophic fungi make up a lower proportion of their relative abundance within fungal communities (Berdugo et al., 2020; Feng et al., 2022). Generally, drought constrains the growth of saprotrophic fungi, thus negatively impacting Collembola feeding activities (Peguero et al., 2021; but see Aupic-Samain et al., 2021b, where drought-driven changes in litter quality and fungal biomass did not alter Collembola densities). Therefore, Collembola face increased scarcity of saprotrophic diets under warm and dry conditions, which could then cause declines in their populations (Aupic-Samain et al., 2021a) and the functions they provide through their feeding (Peguero et al., 2019).

Besides resource scarcity (similar to that in warm-wet conditions, though via different mechanisms), collembolans exposed to warm-dry conditions have to further endure abiotic stress. To mitigate such stress, a Collembola species can migrate vertically in the soil profile to track benign moisture conditions (Holmstrup and Bayley, 2013) and

possibly access saprotrophic diets. However, this strategy will not be sufficient when deeper soil layers eventually dry out, and saprotrophic fungi become scarce. Even though soil-dwelling collembolans can survive and remain active under dry conditions (Holmstrup and Bayley, 2013), their populations eventually decline when droughts prevail over extended periods relevant for collembolan growth and reproduction (i.e., several weeks to months; Flórián et al., 2019). Therefore, the combined detrimental effects of abiotic stress and shortage of saprotrophic diets might explain why hemi- and euedaphic Collembola species suffer under increased aridity (Ferrín et al., 2023). Yet, these soil-dwelling collembolans can persist in lower numbers in semi-arid ecosystems via greater reliance on alternative food sources, such as mycorrhizal fungi. Epedaphic Collembola, through their greater abilities to disperse horizontally (up to 90–120 cm/min; Hågvar, 2000; Zhang et al., 2017), could temporarily find suitable microhabitats with higher moisture and food abundance, rescuing their populations during drier conditions (Chauvat et al., 2014; Ponge, 2020). Overall, we posit that both Collembola and saprotrophic fungi strongly decline in warm-dry conditions given that water limitation represents an important stressor for both

**Table 1**

Summary of documented feeding interactions and feeding preferences of three ecological groups of Collembola (based on their spatial niche in the soil) on various saprotrophic and mycorrhizal fungal species. The fungal species reported on the table are based on the following criteria, depending on the approach taken by each individual study to assess Collembola feeding interactions: (1) the most preferred fungal species in feeding choice experiments, (2) the fungal species providing the highest fitness in no-choice life-history experiments, and (3) the predominant fungal species ingested in observational studies. These interactions were reviewed based on a systematic literature search performed on January 09, 2023 on ISI Web of Science. We retrieved a total of 247 studies using the following search terms: “collembola”; “springtail”; “collembolan” AND “saprotrophic fungi”; “saprophyte”; “saprophytic fungi”; “saprotroph”; “saprobe”; “mycorrhizal fungi”; “mycorrhizae”; “ectomycorrhizal fungi”; “ectomycorrhizae”; “endomycorrhizae”; “endomycorrhizal fungi”; “arbuscular mycorrhizae”; “arbuscular mycorrhizal fungi”.

Collembola group	Collembola species	Fungal group	Preferred fungal species	Study approach	# assessed fungal species	Reference
<b>Epigeic</b>	<i>Entomobrya nivalis</i> , <i>Orchesella flavescens</i> , <i>Pogonognathellus longicornis</i>	<b>Saprotrophic fungi</b>	<i>Cladosporium oxysporum</i> , <i>Penicillium glaucoalbidum</i> , <i>Didymella pomorum</i>	Observational field study in a boreal forest.	–	<a href="#">Anslan et al. (2016)</a> Soil Biology & Biochemistry
		<b>Saprotrophic fungi</b>	<i>Alternaria infectoria</i> , <i>Cladosporium herbarum</i>	Choice experiment between saprotrophic and root pathogenic fungi.	#8	<a href="#">Jørgensen et al. (2003)</a> Biol Fertil Soils
	<i>Pseudosinella alba</i>	<b>Saprotrophic fungi</b>	<i>Alternaria infectoria</i>	Choice experiment between saprotrophic and root pathogenic fungi.	#8	<a href="#">Jørgensen et al. (2003)</a> Biol Fertil Soils
	<i>Heteromurus nitidus</i>	<b>Saprotrophic fungi</b>	<i>Alternaria infectoria</i> , <i>Cladosporium herbarum</i>	Choice experiment between saprotrophic and root pathogenic fungi.	#8	<a href="#">Jørgensen et al. (2003)</a> Biol Fertil Soils
			<i>Alternaria infectoria</i>	No-choice life-history experiment with saprotrophic fungi.	#3	<a href="#">Jørgensen et al. (2008)</a> Applied Soil Ecology
		<b>Mycorrhizal fungi</b>	<i>Laccaria laccata</i> (EMF)	No-choice life-history experiment with one species of EMF and saprotrophic fungi.	#4	<a href="#">Scheu and Folger (2004)</a> Functional Ecology
			<i>Gigaspora gigantea</i> (AMF; the other tested species was not consumed)	No-choice population experiment, including fatty acid analysis, with AMF.	#2	<a href="#">Caravaca and Ruesch (2014)</a> Soil Biology & Biochemistry
	<i>Isotoma anglicana</i>	<b>Saprotrophic fungi</b>	<i>Alternaria infectoria</i>	Choice experiment between saprotrophic and root pathogenic fungi.	#8	<a href="#">Jørgensen et al. (2003)</a> Biol Fertil Soils
	<i>Xenylla grisea</i>	<b>Mycorrhizal fungi</b>	No preference among several <i>Glomus</i> species and <i>Entrophospora schenkii</i> (AMF)	Choice experiment with AMF.	#5	<a href="#">Thimm and Larink (1995)</a> Biol Fertil Soils
	<b>Hemiedaphic</b>	<i>Folsomia candida</i>	<b>Saprotrophic fungi</b>	<i>Teunomyces kruisii</i> (yeast)	Observational field study in a boreal forest.	–
			<i>Cladosporium cladosporioides</i> , <i>Epicoccum purpurascens</i>	Choice experiment between saprotrophic fungi growing on different substrates.	#8	<a href="#">Klironomos et al. (1992)</a> Soil Biology and Biochemistry
			<i>Alternaria alternata</i>	Choice experiment between saprotrophic and AM fungi.	#3; #8; #3	<a href="#">Klironomos and Kendrick (1996)</a> Biol Fertil Soils; <a href="#">Klironomos et al., 1999</a> Functional Ecology; <a href="#">Klironomos and Ursic, 1998</a> Biol Fertil Soils
			<i>Resinicium bicolor</i> , <i>Phanerochaete velutina</i>	No-choice population experiment with saprotrophic fungi.	#4	<a href="#">Tordoff et al. (2008)</a> Soil Biology and Biochemistry
			No differences among <i>Cladosporium cladosporioides</i> , <i>Mucor plumbeus</i> and <i>Alternaria alternata</i>	No-choice life-history experiment with saprotrophic fungi.	#3	<a href="#">Potapov et al. (2013)</a> Ecological Research
			<i>Cladosporium herbarum</i> , <i>Absidia glauca</i>	Choice and no-choice life-history experiment with saprotrophic fungi.	#4	<a href="#">Hedéneč et al. (2013)</a> European Journal of Soil Biology
			<i>Mucor hiemalis</i>	Choice and no-choice life-history experiment with saprotrophic fungi.	#7	<a href="#">Scheu and Simmerling (2004)</a> Oecologia
			<i>Resinicium bicolor</i>	No-choice population dynamics experiment with several cord-forming saprotrophic fungi.	#5	<a href="#">A' Bear et al. (2012)</a> Global Change Biology
			<i>Penicillium hordei</i> (highest fitness)	Choice and no-choice life-history experiment with saprotrophic and AMF fungi.	#4	<a href="#">Larsen et al. (2008)</a> Soil Biology and Biochemistry
			<b>Mycorrhizal fungi</b>	<i>Suillus spraguei</i> (EMF)	Choice experiment between EMF.	#5

(continued on next page)

Table 1 (continued)

Collembola group	Collembola species	Fungal group	Preferred fungal species	Study approach	# assessed fungal species	Reference
			<i>Glomus etunicatum</i> (AMF)	Choice experiment between AMF.	#5	Thimm and Larink, 1995 Biol Fertil Soils
			<i>Glomus intraradices</i> (AMF; most preferred)	Choice and no-choice life-history experiment with saprotrophic and AMF fungi.	#4	Larsen et al. (2008) Soil Biology and Biochemistry
	<i>Folsomia fimetaria</i>	<b>Saprotrophic fungi</b>	<i>Alternaria infectoria</i>	Choice experiment between saprotrophic and root pathogenic fungi.	#8	Jørgensen et al. (2003) Biol Fertil Soils
			<i>Alternaria infectoria</i>	No-choice life-history experiment with saprotrophic fungi.	#3	Jørgensen et al. (2008) Applied Soil Ecology
			<i>Penicillium hordei</i> (highest fitness)	Choice and no-choice life-history experiment with saprotrophic and AMF fungi.	#4	Larsen et al. (2008) Soil Biology and Biochemistry
		<b>Mycorrhizal fungi</b>	<i>Glomus invermaium</i> (AMF; most preferred)	Choice and no-choice life-history experiment with saprotrophic and AMF fungi.	#4	Larsen et al. (2008) Soil Biology and Biochemistry
	<i>Folsomia penicula</i>	<b>Saprotrophic fungi</b>	<i>Alternaria alternata</i>	Choice experiment between saprotrophic and AMF.	#3	Klironomos and Kendrick (1996) Biol Fertil Soils
	<i>Sinella coeca</i>	<b>Mycorrhizal fungi</b>	<i>Glomus intraradices</i> (AMF)	Choice experiment between AMF.	#5	Thimm and Larink, 1995 Biol Fertil Soils
	<i>Sinella tenebricosa</i>	<b>Saprotrophic fungi</b>	No differences among <i>Cladosporium cladosporioides</i> , <i>Mucor plumbeus</i> and <i>Alternaria alternata</i>	No-choice life-history experiment with saprotrophic fungi.	#3	Potapov et al. (2013) Ecological Research
	<i>Proisotoma minuta</i>	<b>Saprotrophic fungi</b>	<i>Phanerochaete velutina</i>	No-choice population experiment with saprotrophic fungi.	#4	Tordoff et al. (2008) Soil Biology and Biochemistry
	<i>Proisotoma minuta</i>	<b>Mycorrhizal fungi</b>	<i>Suillus luteus</i> (EMF)	Choice experiment with EMF.	#4	Hiol et al. (1994)
			<i>Glomus intraradices</i> (AMF)	Choice experiment with AMF.	#5	Thimm and Larink, 1995 Biol Fertil Soils
<b>Euedaphic</b>	<i>Protaphorura armata</i>	<b>Saprotrophic fungi</b>	<i>Alternaria infectoria</i>	Choice experiment between saprotrophic and root pathogenic fungi.	#8	Jørgensen et al. (2003) Biol Fertil Soils
			<i>Aspergillus niger</i>	Observational field study in an agricultural field.	–	Jørgensen et al. (2005) Biology Letters
			<i>Alternaria infectoria</i>	No-choice life-history experiment with saprotrophic fungi.	#3	Jørgensen et al. (2008) Applied Soil Ecology
			<i>Phanerochaete velutina</i>	No-choice population experiment with saprotrophic fungi.	#4	Tordoff et al. (2008) Soil Biology and Biochemistry
			<i>Mucor hiemalis</i> , <i>Cladosporium cladosporioides</i>	Choice and no-choice life-history experiment with saprotrophic fungi.	#7	Scheu and Simmerling (2004) Oecologia
			<i>Coprinopsis picacea</i> , <i>Phallus impudicus</i>	No-choice population dynamics experiment with cord-forming saprotrophic fungi.	#5	A' Bear et al. (2012) Global Change Biology
	<i>Protaphorura fimata</i>	<b>Mycorrhizal fungi</b>	<i>Glomus manihotis</i> (AMF)	Choice experiment with AMF.	#5	Thimm and Larink (1995) Biol Fertil Soils
			<i>Gigaspora gigantea</i> (AMF; the other tested species was not consumed)	No-choice population experiment, including fatty acid analysis, with AMF.	#2	Caravaca and Rues (2014) Soil Biology & Biochemistry
	<i>Tullbergia clavata</i>	<b>Saprotrophic fungi</b>	<i>Alternaria alternata</i>	Choice experiment between saprotrophic and AMF.	#3	Klironomos and Kendrick (1996) Biol Fertil Soils

trophic groups (Blankinship et al., 2011; Manzoni et al., 2012; Wang et al., 2022). Hemiedaphic and especially euedaphic Collembola species could be forced to switch their diets more often, whereas epedaphic species are likely to rely on their greater dispersal abilities to migrate horizontally and access their preferred food sources (Chauvat et al., 2014).

### 3.4. Collembola-mycorrhizal fungal feeding interactions (warm-dry conditions)

Deeper soil dwelling euedaphic Collembola rely more on mycorrhizal food sources compared to epedaphic and hemiedaphic species (Potapov et al., 2016a; Fujii et al., 2021). However, in more arid (i.e., warm and dry) conditions even surface-dwelling Collembola will be forced to rely on mycorrhizal diets. This is because mycorrhizal fungi are



found deeper in the soil and sub-soil, where Collembola are more likely to encounter suitable moisture levels in warmer and drier conditions (Holmstrup and Bayley, 2013). Indeed, a recent study on collembolan trophic shifts in response to drought points to a reduced diversity of food sources utilized by epedaphic and hemiedaphic Collembola, with diets more restricted to plant-derived resources such as roots and plant litter (Meyer et al., 2022). This suggests a lower reliance on the typical saprotrophic diet of surface-dwelling Collembola in drought conditions.

Nonetheless, plant responses to drought can also impact collembolan dependence on mycorrhizal fungi if belowground carbon allocation is reduced (Chomel et al., 2019). When the detrimental effects of drought overpower the positive warming effects on host plants, this will most likely cause die-back of ERM and potentially reduce spore production (Augé, 2001). This die-back of ERM provides large quantities of available resources to Collembola, which show a preference for grazing on senescent mycorrhizal hyphae (Kaneda and Kaneko, 2004), as well as could lessen their competitive advantage over the saprotrophic fungi (Tiunov and Scheu, 2005; Bödeker et al., 2016). Furthermore, this reduction in mycorrhizal biomass may only occur during short and infrequent drought periods. Whereas, longer and more frequent drought events will induce more long-term shifts in mycorrhizal community composition to species with more ruderal and stress-tolerant traits (Chagnon et al., 2013; Sayer et al., 2016).

Observations show such shifts in mycorrhizal groups, with drought promoting greater AMF dominance over EMF (Querejeta et al., 2009, 2021). Between families of AMF, studies have suggested that edaphophilic AMF are less abundant in soil communities of arid environments, whereas rhizophilic AMF are more abundant due to their greater tolerance to low soil moisture (Allen et al., 1995; Chaudhary et al., 2014; Weber et al., 2019; Alguacil et al., 2021; Emery et al., 2022). As previously stated, shifts in mycorrhizal community composition can impact the reliability of mycorrhizal fungi as an alternate food source for Collembola. Studies investigating feeding preferences between these two types of AMF taxa show lower feeding preference for rhizophilic species (Caravaca and Ruess, 2014). This may in part be due to morphological differences as rhizophilic AMF species produce smaller quantities of ERM with thicker hyphae which are less available to Collembola (Hart and Reader, 2002). We therefore suspect that drought-induced shifts in mycorrhizal community composition through an increase in the abundance of mycorrhizal fungi with shorter/thicker hyphae, would reduce the presence and availability of palatable mycorrhizal fungi to Collembola (Caravaca and Ruess, 2014). As such, collembolans relying on mycorrhizal fungi, such as euedaphic ones or those which are forced to shift to mycorrhizal diets due to warming and drought, will experience population declines over time.

#### 4. Outlook

Collembola-fungal feeding interactions are an important factor influencing soil ecology (Rusek, 1998; Petersen, 2002; Tiunov and Scheu, 2005). Based on existing evidence of mixed feeding strategies and climatic responses of collembolans and fungi, we suggest that climate warming will shift collembolan feeding within fungal groups according to the prevailing moisture conditions in their habitat. More specifically, we propose that saprotrophic fungi will become less available as a food source, especially in drier conditions, with concomitant negative impacts for collembolan fitness. The underlying causes of such saprotrophic decline differ between wet (faster litter turnover and reduced soil C in the long term) and dry (harsher abiotic conditions and reduced litter inputs) soil conditions (illustrated in Fig. 2). In both scenarios, mycorrhizal fungi are likely to become the alternative food source for Collembola. Moreover, the accessibility of mycorrhizal fungi to Collembola will vary between warm-wet soil conditions (increased ERM and increased proportion of edaphophilic species, more accessible for Collembola feeding) and warm-dry soil conditions (decreased ERM and increased proportion of less accessible rhizophilic species).

We speculate that warming-driven shifts in Collembola species composition will favour species capable of exploiting resources from mycorrhizal diets. Whether such compositional shifts in Collembola would likely contribute to ecosystem functioning as collembolan communities of the past climate merits rigorous investigation. We additionally hypothesize that species from tropical and warm semi-arid ecosystems (e.g., dry grasslands, shrublands) will perform better under mycorrhizal diets than their counterparts from mesic ecosystems, potentially through underlying adaptations to facilitate the frequent consumption of less palatable food sources. We also expect that Collembola diversity from arctic and boreal regions may experience less climate-driven changes in the availability of saprotrophic fungi, given that soils from these regions host abundant C substrates that could be readily used for the growth of saprotrophs (Feng et al., 2022). Conversely, Collembola diversity from tropical and semi-arid ecosystems are more likely to suffer from shortage of saprotrophs and could be forced to switch more often to mycorrhizal diets. Regardless of their geographical origin, we propose that Collembola species occasionally feeding on mycorrhizal fungi, such as euedaphic Collembola, will forage more frequently on mycorrhiza than species for which the consumption of mycorrhiza is rare, such as epedaphic Collembola (Fujii et al., 2021; Potapov et al., 2021).

Finally, we recommend for a greater implementation of emerging methods for the study of trophic interactions in soil communities (such as stable isotope or molecular gut content analysis; reviewed in Potapov et al., 2022) with the aim to characterise and, if possible, quantify potential dietary shifts of Collembola under experimental climatic manipulation. We believe that the proposed scenarios of Collembola-fungal feeding interactions will help stimulate testable hypotheses for future studies investigating feeding interactions between Collembola and fungi, and their subsequent effects on plant communities and ecosystem functioning in response to climate change.

#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Data availability

No data was used for the research described in the article.

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#### Glossary

- Epedaphic/epigeic** Collembola primarily inhabiting the ground surface
- Hemiedaphic** Collembola mainly found in the litter layer, but often found close to the ground surface and in deeper soil layers
- Euedaphic** Collembola predominantly living in the soil
- MF** Mycorrhizal fungi. Comprises all fungi forming generally mutualistic interactions with belowground plant structures, mainly roots (e.g., arbuscular, ericoid and ectomycorrhizal fungi)
- AMF** Arbuscular mycorrhizal fungi, typically associated with herbaceous plant species and characterized by thin hyphae typically found in organic and mineral soil layers



- EMF** Ectomycorrhizal fungi, typically associated with woody plant species and characterized by thick hyphae typically found in organic soil layers
- ERM** Extraradical mycelium; a collection of mycorrhizal filamentous hyphal structures extending outside of the roots of the host plant and into the soil
- RLC** Root length colonization, proportion of the host plants root colonised by mycorrhizal structures
- Edaphophilic AMF** AMF species possessing traits associated with a competitive life history strategy (e.g., Gigasporaceae)
- Rhizophilic AMF** AMF species possessing traits associated with a stress-tolerant life history strategy (e.g., Glomeraceae)

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