

1 **Title:** Increasing temperature and decreasing specific leaf area amplify centipede predation
2 impact on Collembola

3

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19

20 **Abstract**

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

41

42 **Keywords:** climate change; Chilopoda; plant functional trait; predator-prey interaction;
43 springtail

44

45 **1. Introduction**

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

54 Collembola, among the most widespread and abundant group of soil organisms [13],
55 plays a major role in soil functioning [14] by regulating the microbial (bacterial and fungal)
56 communities, litter decomposition process and nutrient cycling, and consequently feedback on
57 plants [15, 16, 17, 18]. Collembola are also strongly top-down controlled by many predators
58 including spiders [18, 19], centipedes [20, 21] or mites [22, 23]. Furthermore, Collembola are
59 often under the influence of habitat structure as plant litter physical characteristics and quantity
60 (i.e. litter thickness) provide niches serving as microhabitats for Collembola [9, 19, 21, 24].
61 This habitat structure also acts as an important driver of prey-predator interactions by
62 influencing encounter probabilities between Collembola and their predators [19, 21].

63 As Collembola are also extremely sensitive to environmental conditions [13], increasing
64 temperature and decreasing precipitation induced by ongoing climate change [25, 26, 27] can
65 have strong direct impacts on Collembola demographic parameters (e.g. reproduction,
66 development and survival) by altering both soil temperature and moisture conditions [28, 29,
67 30]. As ectothermic organisms, Collembola and their predators generally exhibit greater activity
68 with warming because of elevated metabolic demands [31]. Several experimental field studies,
69 simulating the impact of future climatic conditions in grassland and forest ecosystems, reported

70 a decline in Collembola abundance and diversity in warmer and drier soil conditions, whereas
71 they increased in warmer and wetter soils [9, 30, 32, 33, 34]. While there is a recent wealth of
72 literature on warming effect on prey-predator interactions [26, 35, 36, 37], few attempts have
73 been made on belowground organisms. For example Thakur et al. [23] reported that predatory
74 mites (*Hypoaspis aculeifer* and *H. miles*) reduced Collembola coexistence (*Folsomia candida*
75 and *Proisotoma minuta*) with increasing temperature.

76 In addition, the ongoing climate change can also indirectly affect Collembola by altering
77 litter physical characteristics and quantity produced by plants with thus cascading effects on
78 both the food resource and microhabitat availability for Collembola as well as the outcome of
79 their interactions with predators. In fact, climatic conditions strongly control leaf traits and
80 consequently induce changes in litter traits [38, 39, 40]. Plants under warmer and drier climates
81 tend to have thicker leaves (i.e. sclerophylly) and lower specific leaf area (SLA) in order to
82 reduce water loss [40, 41]. For example, Graça and Poquet [42] reported that SLA of *Quercus*
83 *robur* and *Alnus glutinosa* leaves decreased with increasing temperature across a wide
84 European climatic gradient. As a consequence, for hemi- and epedaphic Collembola (i.e. living
85 on the soil surface and in the leaf litter), this decrease in SLA could imply (i) a lower surface
86 area for fungal colonization leading to a reduced fungal grazing, as well as (ii) less spatial
87 refuges and higher probability to encounter their predators. However, to our knowledge, no
88 previous study attempted to evaluate the consequences of a decrease in SLA on Collembola
89 populations and their interactions with predators.

90 Thus, our current understanding of soil organisms' responses to climate change drivers
91 is still limited by a lack of studies addressing conjointly both direct and indirect effects of
92 climate change on these organisms and their interactions. To address this gap, we designed a
93 full factorial experiment in order to evaluate how the increase of atmospheric temperature (15
94 °C, 20 °C and 25 °C), the decrease of SLA (15.9 ± 0.5 vs. 11.7 ± 0.3 mm².mg⁻¹) of European

95 oak leaves (*Quercus robur* L.) and the presence or absence of a centipede predator (Chilopoda:
96 Lithobiidae) affect the abundance of *Folsomia candida* (Collembola: Isotomidae) in a 5-week
97 microcosm experiment. The elevated temperature treatments were established in order to
98 represent moderate (+5 °C) to high (+10 °C) climate warming scenarios [27], whereas the
99 lowest temperature treatment was based on the climate at which *F. candida* was thermally
100 acclimated (i.e. 15 °C). The decrease of SLA was established to simulate the impact of lower
101 surface area for a same litter mass leading to an alteration of habitat structure. Previous to the
102 experimentation, we carefully checked that the two oak litters (high and low SLA) only differed
103 in their physical traits and not on their chemical traits (i.e. C:N ratio and phenolic
104 concentration). We hypothesized that increasing temperature would induce higher predation
105 effects on *F. candida*, as both prey and predator become more active and must encounter each
106 other more frequently. We also hypothesized that decreased SLA would induce higher
107 predation effects on *F. candida*, as a decrease in habitat complexity provides less spatial refuges
108 for the prey population. Finally, the combination of both direct (i.e. temperature) and indirect
109 (i.e. habitat structure) effects of climate change would conjointly strengthen the top-down
110 control of predator on *F. candida*.

111

112 **2. Materials and Methods**

113

114 **2.1. Material collection**

115

116 **2.1.1. Leaf litter**

117 The experiment was conducted using leaf litter of a common and widespread deciduous
118 tree in temperate European forest: the European oak (*Quercus robur* L.). Freshly-abscised
119 shade leaves were collected on 5 individuals during the litter fall period (autumn 2016) in the

120 Paimpont Forest (48°01'N, 2°10'W) and in the Rennes Forest (48°11'N, 1°34'W),
121 northwestern France. In February 2017, 200 g of the leaf litter from both forests were enclosed
122 in 0.5-mm mesh size litterbags and put on the litter layer under oak trees of the University of
123 Rennes 1 campus (48°07'N, 1°38'W) in order to allow litter microbial colonization. Litter
124 samples were collected after 2 months, dried at 40 °C for 48 h and frozen at -18 °C for 48 h in
125 order to remove animals, and then stored in a dark room at ambient temperature until the start
126 of the experiment.

127 Ten leaves were used to determine the specific leaf area (SLA) of *Q. robur* leaves for
128 each forest. SLA was calculated as the ratio between leaf area and leaf dry weight and
129 determined by weighing (± 0.01 mg) 3 leaf disks obtained with a cork borer (10 mm diameter)
130 from the 10 randomly chosen leaves [42]. The leaf dry weight was determined after drying leaf
131 samples at 60 °C for 48 h. Oak leaves of Paimpont Forest showed a mean SLA of 15.9 ± 0.5
132 $\text{mm}^2.\text{mg}^{-1}$ (thereafter high SLA) while those of Rennes Forest showed a significant 26% lower
133 SLA with a mean of $11.7 \pm 0.3 \text{ mm}^2.\text{mg}^{-1}$ (thereafter low SLA) (t -test = 7.0, $P < 0.001$). In
134 addition to SLA, C:N ratio and phenolic concentration of the two litter types were measured as
135 these two plant functional traits were reported to also influence Collembola population
136 dynamics [9, 24, 43]. Carbon and N concentrations were determined by thermal combustion
137 using a CN analyzer. Phenolic concentration was measured colorimetrically using the method
138 described in Santonja et al. [44] with gallic acid as a standard. Leaf litter types of high and low
139 SLA showed no significant difference in both C:N ratio (37.6 ± 0.6 vs. 40.6 ± 1.1 , respectively;
140 t -test = -2.3, $P = 0.063$) and phenolic concentration (49.3 ± 0.8 vs. $51.8 \pm 0.9 \text{ mg.g}^{-1}$,
141 respectively; t -test = -1.8, $P = 0.123$). As our research hypothesis was based on a physical effect
142 of *Quercus* litter on predator-prey interaction (i.e. habitat structure) and not on a chemical effect
143 of this litter (i.e. trophic or toxic role), we considered that we used two litter types exhibiting
144 similar chemical properties but distinct physical properties to perform our experiment.

145

146 2.1.2. *Collembola and centipede*

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

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

167

168 2.2. *Experimental setup*

169 We tested the effects of three temperatures (15 °C, 20 °C, and 25 °C), two SLA (low vs.
170 high) and centipede predation (no predator vs. predator presence) on Collembola abundance in
171 a full factorial experiment. Each combination was replicated 7 times and then led to the
172 construction of 84 microcosms, i.e. 3 temperatures × 2 SLA × 2 predation levels × 7 replicates.
173 Plastic boxes (12 cm diameter × 10 cm height covered by a nylon net to allow air circulation)
174 were used as microcosms. Each microcosm was filled with 2 g (dry mass) oak leaf litter. In
175 order to keep the base of microcosm moist, litter was added on top of a double layer of filter
176 paper. In order to make the litter adequately moist and to stimulate microbial growth, 50 mg of
177 yeast in 5 mL of deionized water were added on top of the litter 4 days before animals were
178 added. Thirty individuals of *F. candida* were added into each of 84 microcosms at the start of
179 the experiment. In order to allow prey acclimation to leaf litter habitat, one centipede individual
180 was added 2 days after *F. candida* in each treatment including a predator (i.e. 42 microcosms).

181 The experiment was performed during 5 weeks in climate-controlled rooms (Percival
182 AR-41L3) with a 12 h: 12 h light: dark photoperiod, a constant temperature (15 °C, 20 °C or
183 25 °C), and a constant 80% air humidity as centipedes are very sensitive to desiccation [47, 48].
184 The microcosms were kept moist by adding 1 ml of deionized water every 2 days. The 15 °C
185 treatment corresponded to the Collembola culture temperature, the 20 °C and 25 °C treatments
186 to a +5 °C and +10 °C increase, respectively. The two SLA levels (15.9 ± 0.5 vs. 11.7 ± 0.3
187 $\text{mm}^2 \cdot \text{mg}^{-1}$) were used in order to simulate the impact of a reduction in leaf surface area (i.e.
188 31800 vs. 23400 mm^2 for 2 g of oak leaf litter) on Collembola fitness and Collembola-centipede
189 interaction. At the end of the experiment, centipedes were removed by hand and leaf litter of
190 each microcosm was placed on a Berlese-Tullgren funnel to collect Collembola. Individuals
191 were harvested in 90% ethanol and then counted under a stereomicroscope.

192

193 **2.3. Statistical analyses**

194 Statistical analyses were performed using R software (version 3.4.2). A generalized
195 linear model (GLM), followed by post-hoc multiple comparisons (Tukey contrasts), was used
196 to test for the effect of temperature, SLA, centipede predation, and their interactions on
197 Collembola abundance. We fitted the GLM model specifying a Poisson error distribution and
198 log link function because the response variable was count data (i.e. number of Collembola per
199 microcosm).

200

201 **3. Results**

202 Temperature, SLA and predation treatments had significant effects on Collembola
203 abundance (Table 1, Fig. 1). On the whole experiment, we found that Collembola abundance
204 was the highest at 20 °C and the lowest at 25 °C (Fig. 1a). For SLA, Collembola abundance
205 was higher with high SLA than with low SLA (Fig. 1b). Lastly, predation treatment also altered
206 Collembola abundance with higher Collembola abundance in absence of predator (Fig. 1c).
207 However, significant interactions between temperature and predation treatments, between SLA
208 and predation treatments, and between the three treatments were observed (Table 1).

209 The interaction between temperature and predation treatments suggested that increasing
210 temperature differentially affected Collembola abundance with or without a predator (Table 1,
211 Fig. 2). Without predator, +5 °C favored Collembola abundance (+27% compared to 15 °C)
212 whereas +10 °C negatively affected Collembola abundance (-18% compared to 15 °C). In
213 presence of a predator, there was no difference in Collembola abundance between 15 °C and
214 20 °C, while Collembola abundance strongly decreased at 25°C (-55% compared to 15 °C).
215 Furthermore, the negative effect of predation increased with increasing temperature, as the
216 density of *F. candida* was reduced by 26%, 34%, and 59% at 15 °C, 20 °C and 25 °C,
217 respectively.

218 The interaction between SLA and predation treatments suggested that the decrease of
219 SLA negatively affected Collembola abundance only in predator presence (Table 1, Fig. 3).
220 Furthermore, the negative effect of predation increased with the decrease of SLA, from a 28%
221 reduction of Collembola abundance at high SLA to a 50% reduction at low SLA.

222 The interaction between temperature, SLA and predation treatments suggested that the
223 combinations of specific temperature and SLA treatments conjointly alter the predator control
224 of Collembola abundance (Table 1). In fact, the greatest top-down control was observed at 20
225 °C on low SLA (i.e. 70% reduction of Collembola abundance, Table 2), while the lowest top-
226 down control was observed at 15 °C on high SLA (i.e. 18% reduction of Collembola abundance,
227 Table 2).

228

229 4. Discussion

230 As expected, Collembola abundance was depressed by the presence of a centipede. This
231 result is in accordance with previous studies, which reported that centipedes have strong
232 negative effects on Collembola abundance [21, 49, 50]. In agreement with our first hypothesis,
233 we demonstrated that predation effects became stronger with increasing temperature, from -
234 26% at 15 °C to -59% at 25 °C. Grgic and Kos [51] reported optimal temperatures for some
235 European Lithobiidae species between 12 °C and 22 °C, while Chitty [52] reported this
236 temperature range for temperate centipede species between 20 °C and 25 °C, suggesting that
237 the centipedes during our experiment were active foragers. As ectothermic organisms, by
238 increasing their activities with increasing temperature because of elevated metabolic demands
239 [31], higher encounter probabilities between Collembola and centipede induced this short-term
240 increase of predation effects. Our result supports the recent findings of Thakur et al. [10] that
241 also highlighted higher predation effects upon Collembola with increasing temperature.
242 Interestingly, we also found an increase in Collembola abundance with +5 °C increase in

243 temperature that could compensate for the predation impact, as we did not observe a difference
244 in Collembola abundances between the treatments at 15 °C and 20 °C in centipede presence
245 (Fig. 2). Our observation of a maximum abundance of *F. candida* at 20 °C is consistent with
246 the general sigmoid curve obtained when considering the response of an organism over the
247 whole temperature range where development may occur [53]. Stam et al. [54] reported a
248 decrease in clutch size (number of eggs) of *F. candida* at temperature exceeding 22 °C
249 compared with temperature around 15 °C. Fountain and Hopkin [45] also reported an optimal
250 temperature for hatching success at 21°C for *F. candida*. However, Collembola abundance was
251 strongly reduced with +10 °C, and this direct negative effect, coupled with centipede presence,
252 induced a strong decline of *F. candida* population.

253 In agreement with our second hypothesis, we also demonstrated that decreasing specific
254 leaf area (SLA) induced higher predation effects on a Collembola population. In line with our
255 findings, two previous short-term experiments at low temperatures revealed the importance of
256 habitat structure for the per capita interaction strengths of generalist predators on their
257 Collembola prey [19, 21]. In a 24 h experiment at 18 °C day: 16 °C night regime, Vucic-Pestic
258 et al. [19] showed a decrease in consumption rate by a spider (*Pardosa lugubris*) on its
259 Collembola prey (*Heteromurus nitidus*) in presence of moss (*Polytrichum formosum*),
260 highlighting the importance of refuge presence for the prey. In a 24 h experiment at 15 °C,
261 Kalinkat et al. [21] reported a decrease in consumption rate of a predator centipede (*Lithobius*
262 *mutabilis*) on its Collembola prey (*H. nitidus*) according to the increase of litter quantity (*Fagus*
263 *sylvatica*), highlighting the importance of habitat size in the encounter probability between a
264 predator and its prey. Kalinkat et al. [21] demonstrated thus that increasing litter quantity
265 reduced the encounter rates by diluting the prey population to lower density. In the present
266 study, in addition to the importance of i) litter presence [19] and ii) litter quantity [21], we
267 demonstrated for the first time the key importance of a leaf morphological trait as a regulating

268 factor of predator-prey interactions in a leaf litter system. In consequence, the litter habitat
269 modifications mediated by decreasing both litter quantity production [55] and leaf litter SLA
270 [42] in response to climate change would conjointly amplify the predatory control of
271 Collembola populations by decreasing refuge availability and increasing the encounter rate with
272 their predators.

273 Finally, we also confirmed our last expectation that both increasing temperature and
274 decreasing SLA conjointly strengthen the top-down control of a centipede predator on a *F.*
275 *candida* population. In fact, the highest top-down effect was observed at the highest temperature
276 coupled with the lowest SLA. A strong decrease of Collembola abundance could, in turn, leads
277 to a negative impact on their predator population with profound repercussions on soil food web
278 structure. Additionally, these soil cascading trophic effects might have consequences for
279 feedback on plants, as the presence and identity of Collembola can influence nutrient
280 availability for plants, plant traits and strategy, with consequences on both plant productivity
281 and reproduction [9, 16, 17, 18]. As species interactions provide the mechanistic link between
282 warming and ecosystem functions [11, 56], our study suggests that predicting the consequences
283 of climate change may be far from trivial and needs to take into account both direct and indirect
284 effects of climate change to better understand the outcome of short-term dynamics of predator-
285 prey interactions.

286

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293

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- 448

449 **Tables**

450

451 **Table 1.** Output of the general linear model testing for the effects of temperature (15°C, 20°C
452 and 25°C), SLA (low *vs.* high), predation (no predator *vs.* predator presence), and their
453 interactions on Collembola abundance. d.f. = degrees of freedom. Chi-squared (χ^2) and
454 associated *P*-values (with the respective symbols * for $P < 0.05$, ** for $P < 0.01$, and *** for P
455 < 0.001) are indicated.

456

457

	d.f.	χ^2	<i>P</i> -value
Temperature (T)	2	121.3	***
SLA (S)	1	7.4	**
Predation (P)	1	22.2	***
T × S	2	0.1	
T × P	2	57.3	***
S × P	1	12.4	***
T × S × P	2	8.9	*

458

459

460 **Table 2.** Collembola abundance (mean \pm SE; n = 7) according to temperature (15°C, 20°C and
461 25°C), SLA (low vs. high), and centipede predation (no predator vs. predator presence)
462 treatments.

463

Temperature	SLA	No predator	Predator
15°C	High	174.4 \pm 13.9	142.7 \pm 11.5
15°C	Low	155.7 \pm 12.1	101.6 \pm 8.9
20°C	High	222.7 \pm 16.2	175.0 \pm 9.0
20°C	Low	195.3 \pm 10.8	100.0 \pm 7.1
25°C	High	144.0 \pm 10.9	73.0 \pm 7.4
25°C	Low	126.9 \pm 8.7	38.1 \pm 7.3

464

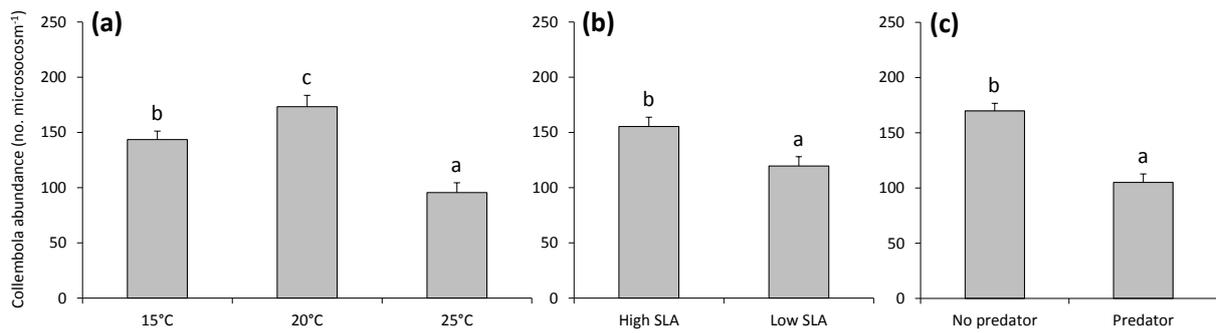
465

466 **Figures**

467

468 **Fig. 1.** Effects of (a) temperature, (b) SLA and (c) predation treatments on Collembola
469 abundance. Each bar represents the mean value \pm SE; $n = 28$ in (a) and $n = 42$ in (b) and (c).
470 Different letters denote significant differences among treatments with $a < b < c$.

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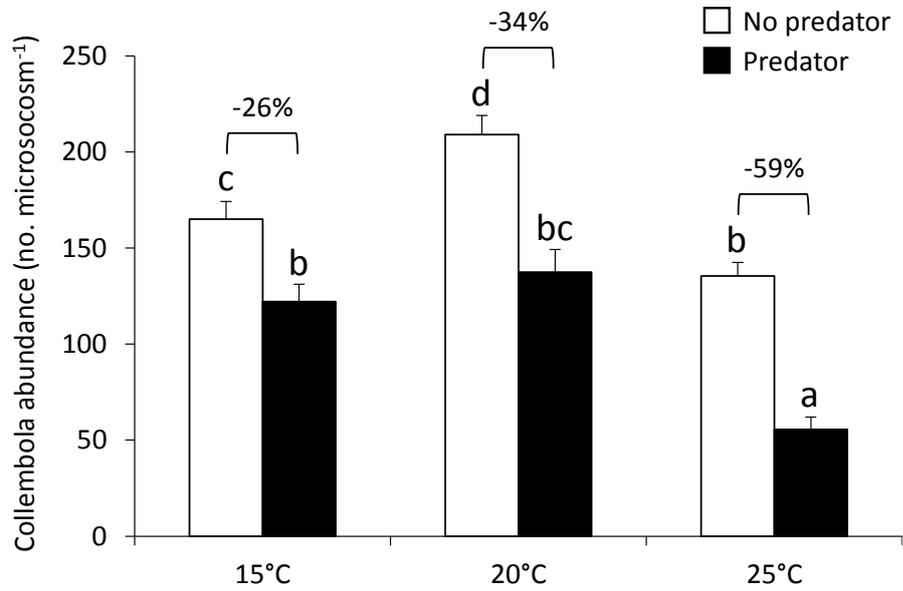


472

473

474 **Fig. 2.** Collembola abundance according to the Temperature \times Predation interaction. Each bar
475 represents the mean value \pm SE; n = 14. Different letters denote significant differences among
476 treatments with a < b < c < d.

477

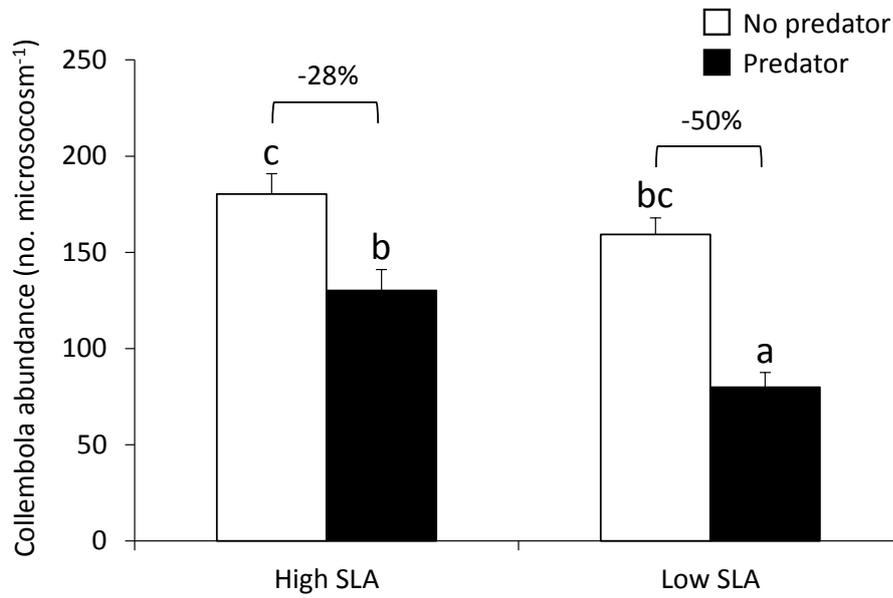


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480 **Fig. 3.** Collembola abundance according to the SLA \times Predation interaction. Each bar
481 represents the mean value \pm SE; n = 21. Different letters denote significant differences among
482 treatments with a < b < c.

483



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485