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Ecophysiological adaptations of genetic lineages of *Parisotoma notabilis* (Schäffer, 1896) (Hexapoda: Collembola): the role of genetic polymorphism in colonization of disturbed habitats

Экофизиологические адаптации генетических линий *Parisotoma notabilis* (Schäffer, 1896) (Hexapoda: Collembola): роль генетического полиморфизма в освоении нарушенных местообитаний

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КЛЮЧЕВЫЕ СЛОВА. ногохвостка, лабораторный эксперимент, эврибионтный вид, экологическая специализация, рудеральный, генетические линии.

ABSTRACT. This study focuses on investigating the ecological specialization of genetic lineages in the widespread eurybiontic springtail species, *Parisotoma notabilis* (Schäffer). Laboratory experiments were conducted to identify biological and ecophysiological differences among the lineages. The results revealed that lineage L1, which dominates disturbed habitats (urban lawns), exhibits greater resistance to high temperatures, desiccation, and heavy metal contamination compared with lineages L2 and L4–Hebert, which prevail in undisturbed habitats (forests). These features of the L1 lineage, as well as the rapid egg maturation rates facilitating successful colonization of disturbed ecosystems. These findings highlight the importance of considering the genetic structure of a species when conducting biomonitoring and ecotoxicological studies. Lineage L1 of *P. notabilis* can be recommended as a test organism for assessing anthropogenic impacts on soil ecosystems.

РЕЗЮМЕ. Исследование посвящено изучению экологической специализации генетических линий широкораспространенного эвритопного вида коллембол *Parisotoma notabilis* (Schäffer, 1896). Провели лабораторные эксперименты, направленные на выявление биологических и экофизиологических различий линий. Результаты показали, что линия L1, доминирующая в нарушенных местообитаниях (городские газоны), обладает устойчивостью к высоким температурам, высыханию и загрязнению тяжелыми металлами по сравнению с линиями L2 и L4–Hebert, преобладающими в ненарушенных местообитаниях (леса). Эти особенности линии L1, а также быстрые темпы созревания яиц, вероятно способствуют успешному освоению нарушенных экосистем. Полученные данные подчеркивают важность учета генетической структуры вида при проведении биомониторинга и экотоксикологических исследований. Линия L1 *P. notabilis* может быть рекомендована в качестве тест-объекта для оценки воздействия антропогенных факторов на почвенные экосистемы.

Introduction

The widespread distribution of certain small soil arthropod species is notable, given their limited mobility and the dense environment they inhabit, which restricts dispersal. Among springtails (Collembola), an example of such a species is the cosmopolitan and eurybiontic

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Parisotoma notabilis (Schäffer, 1896), which reaches high densities in various natural and disturbed habitats [Potapov, 2001; Kuznetsova, 2002]. Notably high populations of *P. notabilis* have been recorded even in areas of soil contaminated by heavy metals [Haimi, Siira-Pietikäinen, 1996; Eitminaviciute, 2006].

Many widespread Collembola species exhibit genetic polymorphisms, with differences between lineages often reaching the species level [Porco *et al*., 2012]. The complex genetic structure of these species may explain their broad geographical distribution and eurybiontic traits. Differences in cold tolerance have been demonstrated for various populations of Collembola, for example in *Orchesella cincta* (Linnaeus, 1758) from different geographical regions of Europe [Bahrndorff *et al*., 2009], and in *Folsomia manolachei* Bagnall, 1939 from caves vs forest litter [Raschmanová *et al*., 2017]. Our study of *P. notabilis* demonstrated that, in Eastern Europe, the lineage L2 was predominantly found in minimally disturbed natural forest, while lineage L1 was almost exclusively found in highly disturbed habitats (lawns and fields), and lineage L4–Hebert exhibited a eurybiontic distribution pattern [Striuchkova, Kuznetsova, 2024].

Laboratory studies of different genetic lineages of the springtail *Folsomia candida* Willem 1902 (ISO 11267) differed in lifespan [Tully, Lambert, 2011], and egg size and clutch size [Tully, Ferrière, 2008]. Such findings are generally considered in an evolutionary context; however, it remains unclear to what extent they may determine distribution across different habitats and resilience to disturbance. Laboratory studies of *P. notabilis*, without regard to genetic lineages, vary widely in their assessment of the impacts of temperature [Thibaud, 1977 vs Malmström, 2008] and heavy metal pollution [Russell, Alberti, 1998 vs Chauvat, Ponge, 2002] on this species.

We hypothesize that the differential distribution of *P. notabilis* genetic lineages along gradients of habitat disturbance is driven by their distinct biological and ecophysiological adaptations. To test this hypothesis, we conducted laboratory observations on egg maturation rates and experiments to assess the effects of elevated and reduced temperatures, desiccation, and heavy metal exposure — ecological factors that distinguish disturbed habitats (e.g., urban lawns) from natural forests.

Material and methods

Material collection. Samples were collected during autumn 2023, as well as in spring and autumn 2024, across various locations in Moscow and the Moscow Oblast. The sampling sites included both natural and anthropogenically disturbed habitats. We assumed based on our previous studies that individuals collected from the lawn habitat represented the L1 lineage, while those from the forest represented the L2 and L4–Hebert lineages [Striuchkova, Kuznetsova, 2024]. At each location, 5-liter samples of litter and/or greensward and topsoil were collected. Springtails were extracted from litter and soil samples into penicillin vials filled with water using the standard Tullgren funnel method over a 24-hour period. The target species was selected under a binocular microscope using a fine brush. Species identification was performed using appropriate taxonomic keys [Potapov, 2001; Fjellberg, 2007].

Collembola maintenance. Collembola were housed in glass vials, either small penicillin vials with a bottom diameter of 2 cm and a height of 5.5 cm or larger vials with a diameter of 3.5 cm and a height of 5 cm. The vials were filled to one-third of their height with a mixture of medical gypsum and activated charcoal in a 9:1 ratio and sealed with plastic caps or watch glasses. The individuals were maintained at 100% humidity and an average temperature of 17 °C (range: 15–18 °C), except in experiments in which these parameters were altered.

For the experiments, a suspension of blue-green algae (*Arthrospira* spp., spirulina) was used as the food source. Its intense coloration makes it possible to assess whether an individual springtails consumes or avoids contaminated food. In addition, baker's yeast was used as food during cultivation [Sharma, Kevan, 1962; Varshav, Davydova, 2014].

Observation of individuals from habitats with varying degrees of disturbance. Survival rates and egg maturation were assessed for seventy-four individuals of the target species from natural and disturbed habitats, which were placed individually in penicillin vials (N = 53 individuals from two mixed forests in the Moscow Oblast, and 20 individuals from three lawns in Moscow and Krasnogorsk).

Survival experiments under different temperature conditions. The elevated exposure temperature ranged from 28–30 °C, and four experimental series were conducted. The reduced temperature was set at 1 °C, with one experimental series conducted. In each series of experiments, five individuals from the lawn and five individuals from the forest were used. Individual springtails were kept in small containers.

Survival experiments under desiccation stress. Each small vial was supplemented with 0.1 g of distilled water (~3 drops) and sealed with fine gauze to allow natural evaporation of moisture at room temperature (24 °C). Observations were conducted every 2–3 h. A total of three series of experiments were conducted: in each series, five individuals from the lawn and five individuals from the forest were used.

Survival experiments with food contaminated with heavy metals (HM). Three experiments were conducted with food contaminated by HM: suspensions with Cu^{2+} at 5 mg/g (two series), Cu^{2+} at 50 mg/g (one series), and Pb^{2+} at 5 mg/g (three series). As a reference for selecting metal concentrations, data from Pedersen *et al*. [2000] were used, where the copper concentration in the food reached 6.4 mg/kg in experiments on *Folsomia candida* and *F. fimetaria* (Linnaeus, 1758). Each experimental series included 20 individuals: 5 ind. from forest cultures on contaminated food, 5 ind. from lawn monocultures on contaminated food, and 5 ind. from each habitat as a control group. In the copper ion experiments, small individual vials were used, while in the lead ion experiments, five individuals were kept together in one large vial.

Genotyping of individuals. Preliminary genetic analysis of forest individuals revealed a mixture of three genetic lineages, with a predominance of L4–Hebert and L2, while individuals of the L1 lineage were found only sporadically. In the experiments, each dead springtail was placed in an individual microtube with 96% ethanol and stored in a refrigerator at 4 °C for subsequent determination of their genetic lineage. Since the fixation of deceased individuals in ethanol could not always be performed promptly, not all individuals were genotyped. The methodology for DNA extraction, PCR amplification of the D3–D5 region of the 28S gene, purification, and sequencing, as well as subsequent bioinformatic data processing, are described in detail by Striuchkova *et al*. [2022].

Statistical analyses. Data analysis and visualization were performed using GraphPad Prism (version 10.2.3)

(https://www.graphpad.com). To assess the significance of differences in egg maturation rates between individuals from natural and disturbed habitats, an unpaired t-test was used. To evaluate the survival of individuals over time in laboratory experiments, the Kaplan-Meier estimator was applied. The significance of differences between two survival curves was assessed using the non-parametric log-rank test.

Results

Molecular analysis showed that individuals from the urban lawn belonged to the L1 lineage, and individuals from the forest - mainly to L2 and L4–Hebert.

Under identical conditions, individuals from the urban lawn survive significantly better in culture, and their egg maturation rate is one-third faster compared to individuals from the forest (both $p << 0.001$) (Figs 1–2).

Individuals from the lawns also demonstrated significantly higher survival rates at elevated temperatures (28–30 °C) and under desiccation stress (both $p = 0.01$, Figs 3–4). At 1 °C, both cultures survived for at least 40 days. Further observations were not conducted.

Forest individuals died when food was contaminated with Cu^{2+} or Pb^{2+} at 5 mg/g ($p = 0.01$ and $p << 0.001$, respectively) (Figs 5–8). Individuals from the lawn were more tolerant (the effect of metals on survival is not reliable; $p > 0.1$). When the concentration of Cu^{2+} was increased tenfold, *P. notabilis* starved: their digestive tracts were empty.

Discussion

Survival in culture and egg maturation rates. Studying the biology of springtails is challenging because species that avoid disturbed habitats are often extremely difficult to cultivate in the laboratory. This is evidenced by the lists of species studied in laboratories, consisting mainly of ruderal and compost species [Hopkin, 1997]. Different genetic lineages of *Parisotoma*

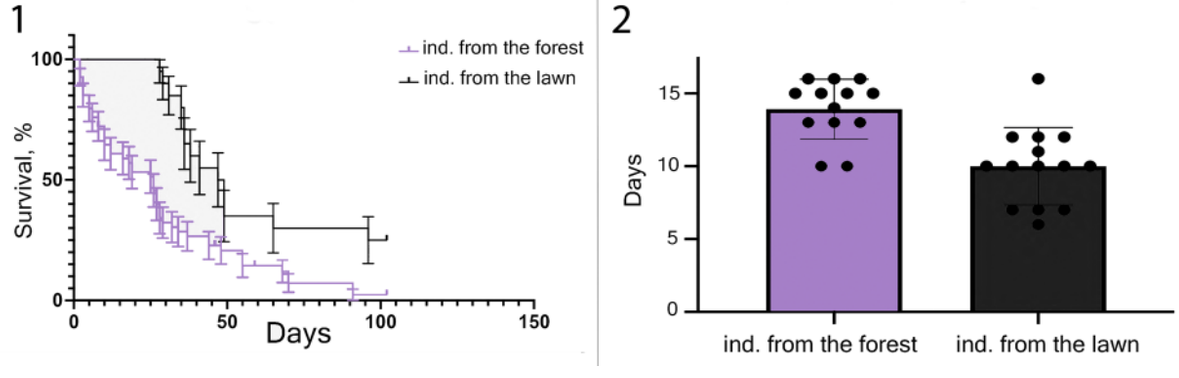

Fig. 1–2. Survival and egg maturation rates of *Parisotoma notabilis* from forests and urban lawns. 100% humidity, 15–18 °C, with spirulina as the food source.
Рис. 1–2. Выживаемость и скорость созревания яиц *Parisotoma notabilis* из лесов и с городских газонов. Влажность 100%, температура 15–18 °C, спирулина в качестве корма.

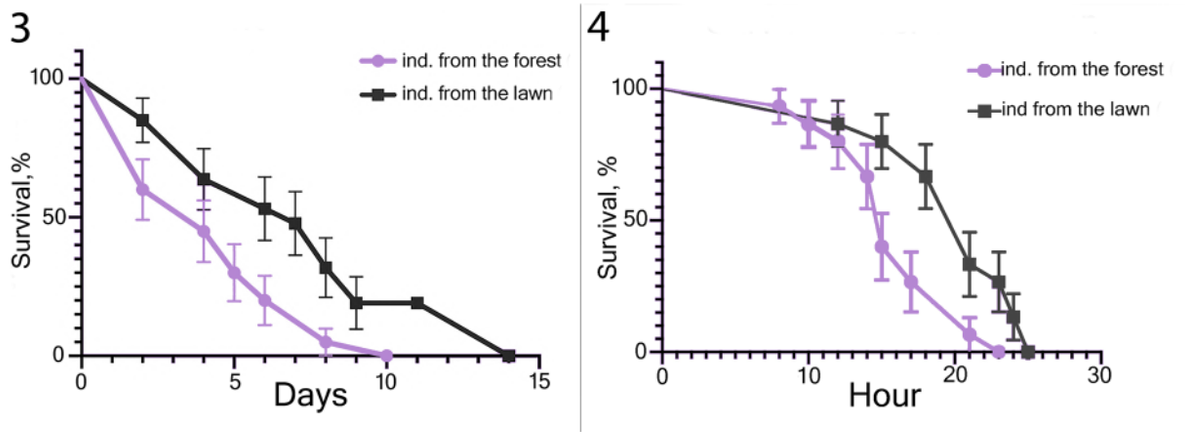

Fig. 3–4. Survival of *Parisotoma notabilis* from forests and urban lawns: 3 — elevated temperature (28–30 °C, 100% humidity); 4 — desiccation stress (24 °C) (n — number of individuals). Spirulina was used as the food source.
Рис. 3–4. Выживаемость *Parisotoma notabilis* из лесов и с городских газонов: 3 — повышенная температура (28–30 °C, 100% влажности), 4 — высыхание (24 °C) (n — количество особей). В качестве корма использовали спирулину.

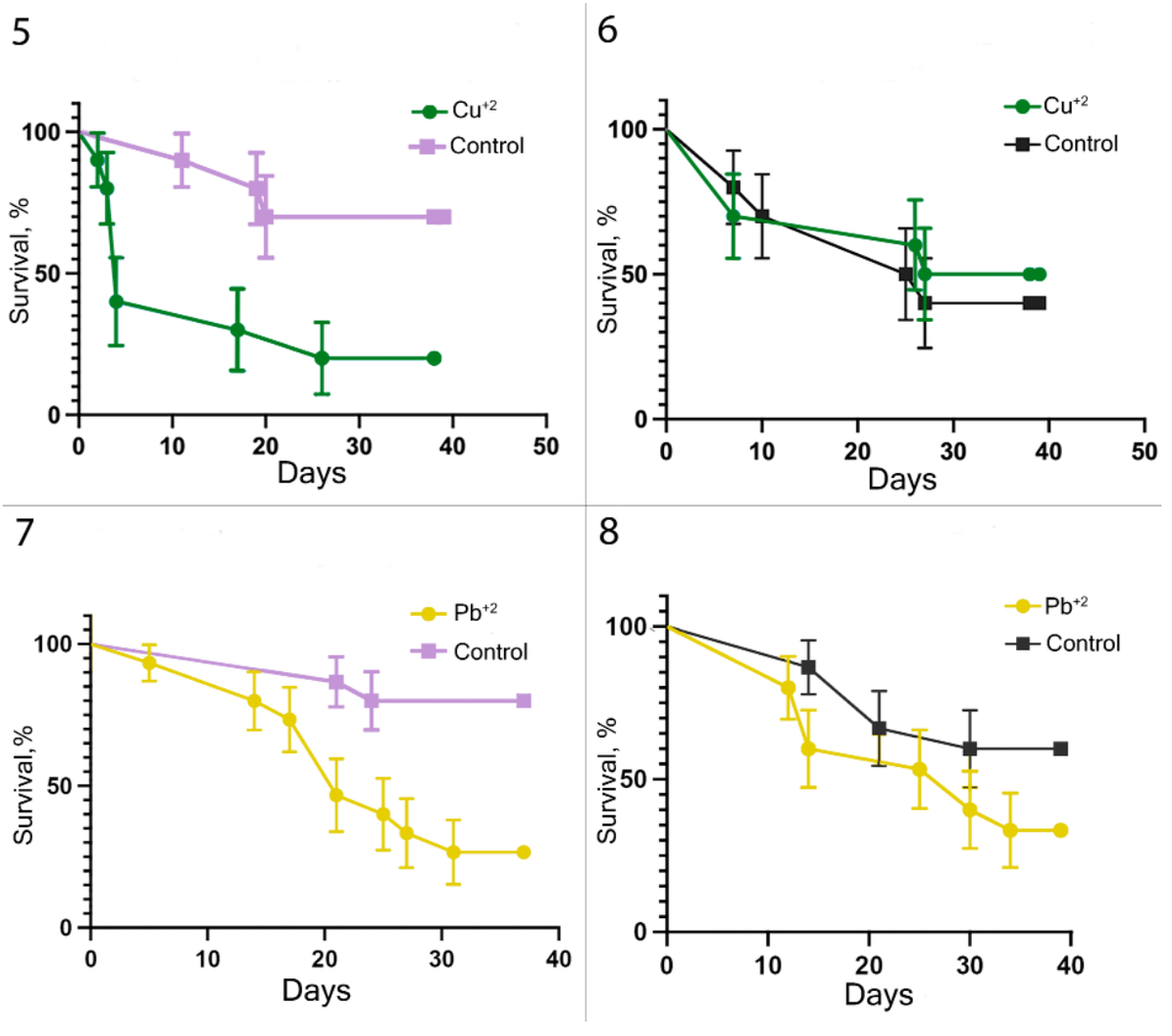

Fig. 5–8. Survival of *Parisotoma notabilis* under food contamination with 5 mg/g: 5, 6 — Cu^{2+}; 7, 8 — Pb^{2+}; 5, 7 — individuals from forest; 6, 8 — from urban lawn. 100% humidity, 15–18 °C in all variants.
Рис. 5–8. Выживаемость *Parisotoma notabilis* при загрязнении корма 5 мг/г: 5, 6 — Cu^{2+}; 7, 8 — Pb^{2+}; 5, 7 — особи из леса; 6, 8 — с городского газона. Во всех вариантах влажность 100%, 15–18 °C.

notabilis behave in the laboratory like distinct species: some resemble species that avoid disturbed habitats, while others are tolerant to such conditions. Sharma and Kevan [1962], who cultivated and studied the life cycle of *P. notabilis*, likely worked with lineage L1, which has a better survival rate in the laboratory.

It has previously been shown that eggs hatch in 7–8 days at 17 °C [Sharma, Kevan, 1962]. In our study, egg maturation in the "fast-maturing" individuals from the lawn took longer (10 days) at similar temperatures (15–18 °C). Nevertheless, the faster egg maturation rates of lineage L1 compared to individuals from the forest are likely to be an important factor in its success in colonizing disturbed habitats.

Effects of elevated and reduced temperatures. Springtails generally tolerate high temperatures poorly, and their survival under such conditions depends heavily on humidity [for example, Block, 1994]. Temperatures of 30–35 °C are critical for most polar springtails [Block, 1994; Hodkinson, 1996], and some heat-tolerant species can survive short periods at 37–40 °C and even higher [Janion-Scheepers *et al*., 2018; Xie *et al*., 2023]. Our results indicate that *P. notabilis* lineages differ in their tolerance to high temperatures: lawn lineage is more tolerant compared to forest lineages. This trait aligns with the ability of lineage L1 to colonize urban lawns [Striuchkova, Kuznetsova, 2024], where soil warms more than in forest biotopes due to litter removal and reduced shading [Dobrovolsky, 1997; Huang *et al*., 2020]. In an earlier study on the effects of temperature on *P. notabilis* conducted in Norway [Malmström, 2008], individuals survived at 30 °C for only 4–12 hours. The forest lineage L2 is characteristic of that region [Saltzwedel *et al*., 2017]. It can be hypothesized that under global climate

warming, lineage L1 will have a competitive advantage over more sensitive forest lineages.

Springtails are relatively resistant to low temperatures [Hopkin, 1997]. Some polar springtails can survive at least at –24 °C [Convey *et al*., 2015], with the lowest recorded supercooling temperature being –38 °C for *Gomphiocephalus hodgsoni* Carpenter, 1908 [Sinclair, Sjursen, 2001]. According to Sharma and Kevan [1963], *P. notabilis* individuals survived for over a month at 0 °C, which is consistent with our data for all lines studied.

Desiccation. Most springtail species thrive at humidity levels of 100–98%, with desiccation resistance varying among different life forms [Stebaeva, 1975]. At 30% humidity, inhabitants of grassy habitats survive for 10 hours, litter-dwellers for 1 hour, and soil-dwellers for 15 mins [Maldwyn-Davies, 1928]. *P. notabilis* belongs to the litter-dwelling group, specifically the lower-litter life form [Stebaeva, 1970]. In our experiments, forest individuals were less resistant to desiccation compared to lawn individuals. This aligns with the widespread distribution of lineage L1 on urban lawns, where humidity fluctuations are more pronounced [Dobrovolsky, 1997; Huang *et al*., 2020].

Effects of heavy metals. In springtails, heavy metals enter the body through food and passively through the body surface due to the absence of a continuous epicuticle [Hopkin, 1997]. In polluted soils, species with a well-developed ability to detect and avoid metals via chemoreception are often abundant [Tranvik, Eijsackers, 1989; Filser *et al*., 2000] and some also have the ability to excrete metals during molting [Humbert, 1979; Joosse, Buker, 1979]. High abundance of the *P. notabilis* has been noted in habitats contaminated with heavy metals [Haimi, Siira-Pietikäinen, 1996; Russell, Alberti, 1998; Eitminaviciute, 2006; Kuznetsova, 2009; Winkler *et al*., 2018]. However, in laboratory experiments, individuals from natural habitats showed sensitivity to relatively low concentrations of copper [Pernin *et al*., 2006] and lead [Chauvat, Ponge, 2002] ions. In our experiments, individuals from the lawn were more resistant to food contaminated with heavy metal ions (copper, lead) than forest lineages, consistent with the literature data.

In summary, individuals from the lawn (lineage L1) thrives in laboratory conditions and survives successfully in more disturbed habitats compared to forest lineages. The lineage L1 exhibits more rapidly maturing eggs (and possibly a shorter life cycle), representing a key life history characteristic of an r-strategist [MacArthur, Wilson, 1967]. The ecophysiological features of lineage L1 (tolerance to elevated temperatures and heavy metal-contaminated food), combined with its r-strategy, can be considered preadaptations to their colonization of disturbed habitats. Possibly, lineage L1, which we have also reported in fields [Striuchkova, Kuznetsova, 2024], expanded its range in concert with the increase in anthropogenically disturbed areas, such as during the Bronze Age (~5000–2500 years ago), when slash-and-burn agriculture spread across most of Europe's forested territories [Udaltsova, 1986].

The differences demonstrated in the ecophysiology of lineages are important to consider when developing indicator-based approaches using springtails. The clear response to disturbance opens opportunities for genetic monitoring of soil decomposer communities using lineage L1 as an indicator [Striuchkova, Kuznetsova, 2024]. However, genotyping of the culture is crucial for obtaining reliable results in biotesting, where *Folsomia candida* is widely used (ISO 11267).

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Conflict of interest

The authors of this work declare that they have no conflicts of interest.

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