

Contrasting phylogeographic patterns in cryptic lineages of *Parisotoma notabilis* (Collembola): Anthropogenic expansion vs. natural diversification

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Received 16 May 2025 | Accepted 14 August 2025 | Published online 1 December 2025

Abstract

Molecular-genetic analysis of two cryptic lineages (L1 and L2) of the parthenogenetic springtail *Parisotoma notabilis* revealed contrasting dispersal patterns across the Holarctic region. Our study demonstrated that lineage L1 is characterized by a “star-like” haplotype network with a dominant global haplotype L1 α , low genetic diversity, expansion across Western Eurasia and association with disturbed habitats. In contrast, lineage L2 displays a complex “web-like” haplotype network, high genetic diversity and preference for natural forest ecosystems. These findings suggest distinct evolutionary histories of cryptic lineages within a single species, which likely were shaped by their ecological divergence.

Keywords Springtail | cryptic diversity | haplotype network | ecological divergence | ecological speciation | cytochrome oxidase I (COI) gene

1 Introduction

Molecular genetic studies continue to reveal extensive cryptic diversity among widespread springtail species, including the parthenogenetic *Parisotoma notabilis* (Schäffer, 1896). This is a cosmopolitan species occurring in all natural zones from lowlands to mountains (Potapov, 2002) and is generally abundant in Europe (Fiera & Ulrich 2012). It shows considerable ecological plasticity and tolerance to anthropogenic disturbance (Kuznetsova, 2002). During the past 10 years, five distinct genetic lineages have been identified in this species, with genetic distances approaching species level (Porco et al. 2012; Saltzwedel et al. 2017; Sun et al. 2018), and the species is now referred to as *P. notabilis* sensu lato. Molecular dating analyses (Saltzwedel et al. 2017) confirm the ancient origin of *P. notabilis* lineages, estimating the

earliest cladogenesis events at approximately 11.5 million years ago. The taxonomic status of these lineages (species or subspecies) remains formally unresolved due to the absence of detectable morphological differences, at least among the widely distributed lineages (L0, L1, L2, L4-Hebert). Morphological studies have revealed minor differences between lineages L1 and L2 in sensory chaetotaxy that require further confirmation from different parts of their ranges (Potapov, 2022).

As molecular studies have expanded to cover a wider geographic range and diversity of habitat types, the number of known lineages has increased to 12 (Porco et al. 2012; Hebert et al. unpublished; Anslan & Tedersoo 2015; Saltzwedel et al. 2017; Lafooraki et al. 2022; Striuchkova et al. 2024). Our recent studies of these lineages have revealed their uneven distribution along urbanization gradients (Striuchkova & Kuznetsova 2024).

The distribution of lineage L1 differs significantly from other lineages, showing a robust correlation with habitat disturbance. It is this lineage that is primarily associated with the global distribution of the species, particularly in the Holarctic region. Specifically, lineage L1 has been reported in North America, Western Europe and Africa (Porco et al. 2012; Saltzwedel et al. 2017), Eastern Europe (Striuchkova et al. 2024) and Asia (Saltzwedel et al. 2017; Lafooraki et al. 2022; Cheng-Wang Huang, personal communication). The other widely distributed lineages are primarily associated with forest habitats (L0, L2) or show broader ecological tolerance (L4-Hebert) (Striuchkova & Kuznetsova, 2024).

In this study, we hypothesize that: (1) the “natural” lineage L2 (prefers natural forest and meadows) and “anthropogenic” lineage L1 (prefers urban and agriculture sites) exhibit distinct geographic distribution patterns; (2) the success of lineage L1 in disturbed Holarctic habitats results from the expansion of a single successful haplotype; (3) the “anthropogenic” lineage, originating ~7.5 million years ago, may have originated in naturally disturbed habitat patches. To address these hypotheses, we investigated the relationships between geographic distribution patterns and biotopic preferences in genetic lineages of *P. notabilis* to assess their potential for ecological speciation.

2 Materials and Methods

To test the first and second hypotheses, we consolidated our own and other available published data to conduct the most comprehensive analysis yet attempted of haplotype networks for the two most widespread *P. notabilis* lineages, L1 and L2. For this purpose, all available nucleotide sequences of the COI gene fragment of *P. notabilis* (716 specimens) were retrieved from GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>) in the “GenBank (full)” format, which includes complete specimen metadata. A custom C# parser (https://github.com/avstru/Genbank_Parser) was used to extract and organize the following data into an Excel table: GenBank accession numbers, specimen identifiers with individual codes, and geographic information (country, location, coordinates). Lineage assignment for each individual was determined by constructing a maximum likelihood phylogenetic tree (T92 + G + I) from the COI gene fragment using MEGA-11 software (v. 11) (Tamura et al. 2021).

The analysis incorporated recently obtained COI sequences from populations in Eastern Europe and the Caucasus region (Striuchkova et al. 2024), publicly available GenBank data from Western Europe, North

America, and Asia Minor, along with one additional L1 lineage sequence from China kindly provided by Cheng-Wang Huang (personal communication). Short sequences (less than 400 nucleotides) were excluded. The main dataset comprised two major transoceanic regions: North America and Western Eurasia, the latter including Europe, the Caucasus region, and the Near East (Table 1). GenBank accession numbers for lineages L1 and L2 are presented in Appendix 1.

Table 1. Number and length (bp) of sequences used for haplotype network analysis.

Lineage	Territory	Our data	GenBank	Total	bp
L1	Western Eurasia	68	168*	372	462
	North America	0	136		
L2	Western Eurasia	20	75	230	438
	North America	0	135		

* including 74 individuals from a single sample from Paris.

For a more detailed analysis of the genetic structure of *P. notabilis* lineages across the Holarctic, collection sites were primarily classified by country. Despite their considerable geographic extent, the studied areas of Russia (European element and Caucasus) and Canada had relatively clustered sampling areas, allowing for further subdivision. Russia was divided into Northern, Central, and Southern locations, plus the Baltic coastal region (Kaliningrad oblast), while Canada was partitioned into Western, Central, and Eastern locations. In total, 27 distinct locations were defined.

To assess the biotopic confinement of haplotypes, specimens with complete collection label records were classified by habitat type as follows: high anthropogenic disturbance (urban lawns), moderate anthropogenic disturbance (urban forest parks), and undisturbed habitats (forests). Additionally, to test the third hypothesis about the origin of lineage L1, a separate group was created for specimens from natural sites, associated with localized natural disturbances. Organically enriched substrates (river floodplain sediments and rotting wood) were considered under this category. In total, data were obtained for 90 L1 individuals and 45 L2 individuals for the analysis of habitat preference.

Nucleotide sequences were aligned using the multiple alignment tool ClustalW implemented in BioEdit v7.2 (Hall, 2011). Haplotype network reconstruction was performed using the TCS algorithm (a statistical parsimony approach) that calculates connection probabilities between haplotypes and infers mutational steps between them. The analysis was implemented in PopART v1.7 ([SOIL ORGANISMS 97 \(3\) 2025](https://</p></div><div data-bbox=)

Table 2. Measures of genetic diversity (mean $\pm$ SD) for lineages L1 and L2 based on mitochondrial cytochrome c oxidase subunit I (COI) sequences.

Lineage	L1			L2		
Region	North America	Western Eurasia	Both regions*	North America	Western Eurasia	Both regions
n	136	236	373	135	95	230
S	8	12	19	16	40	40
k	0.524	0.346	0.422	1.688	2.552	2.151
H	6	11	15	6	26	28
Hd±SD	–	–	0.374 ±0.027	–	–	0.714 ±0.024
π ±SD	0.0015 ± 0.0002	0.0010 ±0.0001	0.0012 ± 0.0001	0.0043 ±0.0004	0.0065 ±0.0007	0.0057 ±0.0006
k between regions	0.461		–	2.427		–

n – number of sequences, S – number of polymorphic sites, k – mean nucleotide differences, H – number of haplotypes, Hd – haplotype diversity, π – nucleotide diversity.

*including China

popart.maths.otago.ac.nz). The sequence alignments were first converted to NEXUS format using DnaSP v6 (<http://www.ub.edu/dnasp/>).

Genetic diversity was quantified using several metrics calculated in DnaSP, including the number of polymorphic sites (S), mean pairwise nucleotide differences (k), haplotype diversity (Hd), and nucleotide diversity (π), with their corresponding standard deviations ($\pm$ SD). Haplotype diversity (Hd) measures the probability that two randomly selected alleles are different, while nucleotide diversity (π) represents the average number of nucleotide differences per site across all pairwise sequence comparisons (Nei, 1987). For each lineage (L1 and L2), we calculated the Jaccard index (J) to assess haplotype set similarity between Western Eurasia and North America: $J = C/(A+B-C)$, where: C = number of haplotypes shared between Western Eurasia and North America; A = haplotypes found only in Western Eurasia; B = haplotypes found only in North America. The index ranges from 0 (no shared haplotypes) to 1 (identical haplotype composition).

To assess the significance of genetic polymorphism and elucidate its nature, we employed Tajima's neutrality test (Tajima 1989), which evaluates deviations of observed polymorphism from expected evolutionarily neutral genetic changes (Tajima, 1989; Ramos-Onsins & Rozas, 2002). The test is based on the premise that sudden population expansions cause characteristic shifts in allele frequency spectra that deviate from expectations under the Wright-Fisher neutral model. Values of $D > 0$ indicate a deficiency of rare alleles (singletons) due to population bottlenecks or balancing selection, while $D < 0$ reflects an

excess of singletons resulting from population growth through fixation of advantageous alleles. All calculations were performed using DnaSP v6.

3 Results

Genetic diversity of lineages

Lineage L1 was characterized by low genetic diversity in haplotypes, polymorphic sites, and nucleotides despite its large sample size. All these measures were substantially higher in lineage L2 (Table 2). In Western Eurasia, both lineages exhibited several times more haplotypes than in North America. The haplotype sets differed markedly between continents, showing only 13 % and 14 % similarity based on the Jaccard index (J) for lineages L1 and L2, respectively. The mean nucleotide differences between regions were significantly greater in lineage L2 compared to L1. However, for lineage L1, this diversity measure was higher in North America than in Western Eurasia, while the opposite pattern was observed for lineage L2 (Table 2).

Haplotype networks

The haplotype network of lineage L1 displayed a “star-like” form with radiating branches and a single central node. This dominant haplotype, found in 287 individuals (77 % of sequences), shows near-global distribution (90 % of sampled locations), being absent only in eastern Canada

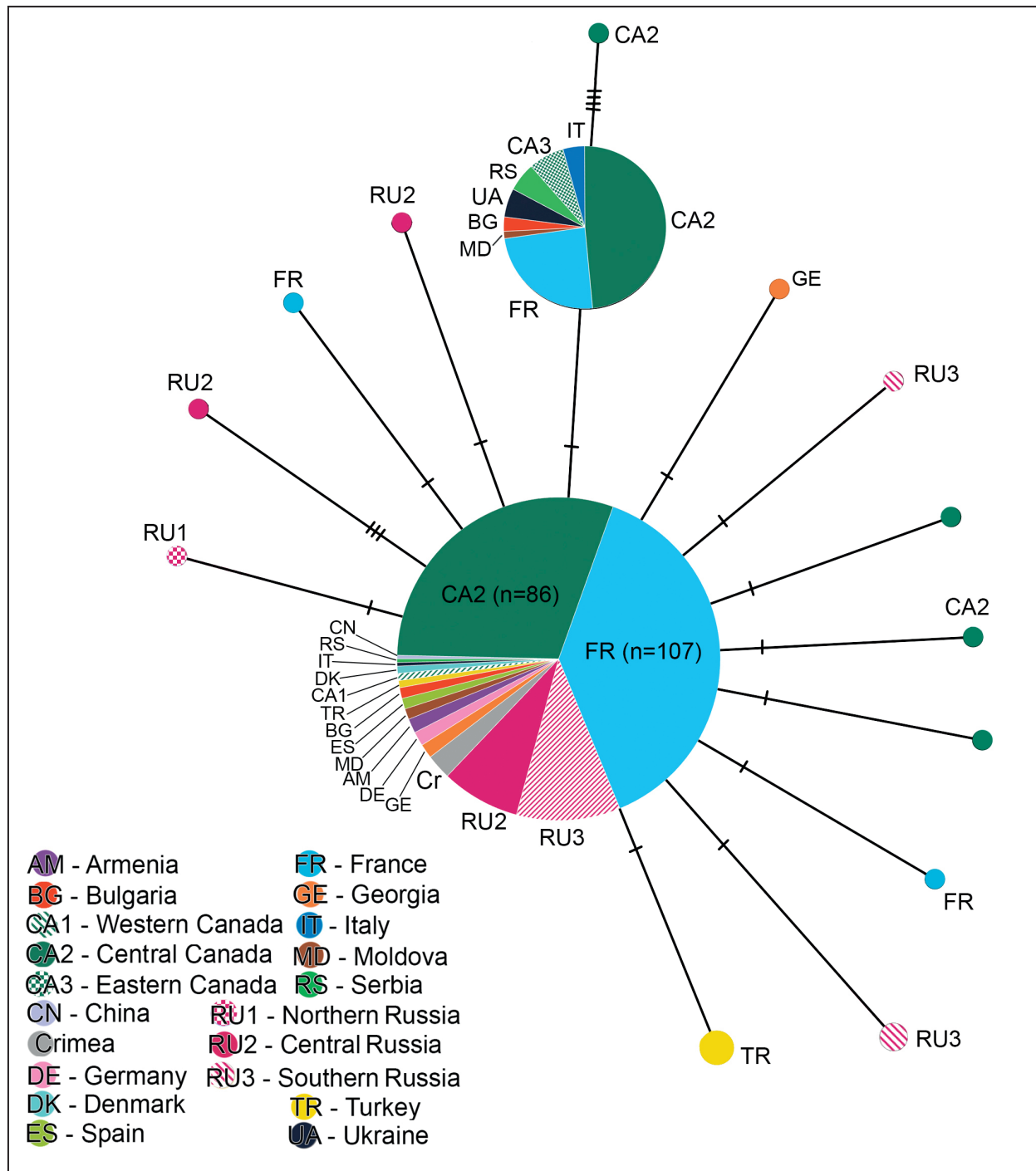


Figure 1. Haplotype network of *P. notabilis* lineage L1 based on 373 COI gene sequences (462 bp) obtained from 20 locations. Haplotype size is proportional to frequency. The number of transverse lines corresponds to mutational steps.

and northern European Russia (Fig. 1). The second most frequent haplotype of this lineage was detected in just eight locations (40%), with all remaining haplotypes having localized distributions. Most haplotypes differed from the central one by a single mutational step. The highest haplotype diversity occurred in the extensively

sampled regions of central Canada (6 haplotypes) and France (4 haplotypes).

The network of lineage L2 had a different “web-like” morphology, reflecting its greater haplotype diversity (Fig. 2). Three haplotypes showed relatively broad distributions and higher frequencies. Notably, central and northern European Russia harbored more haplotypes

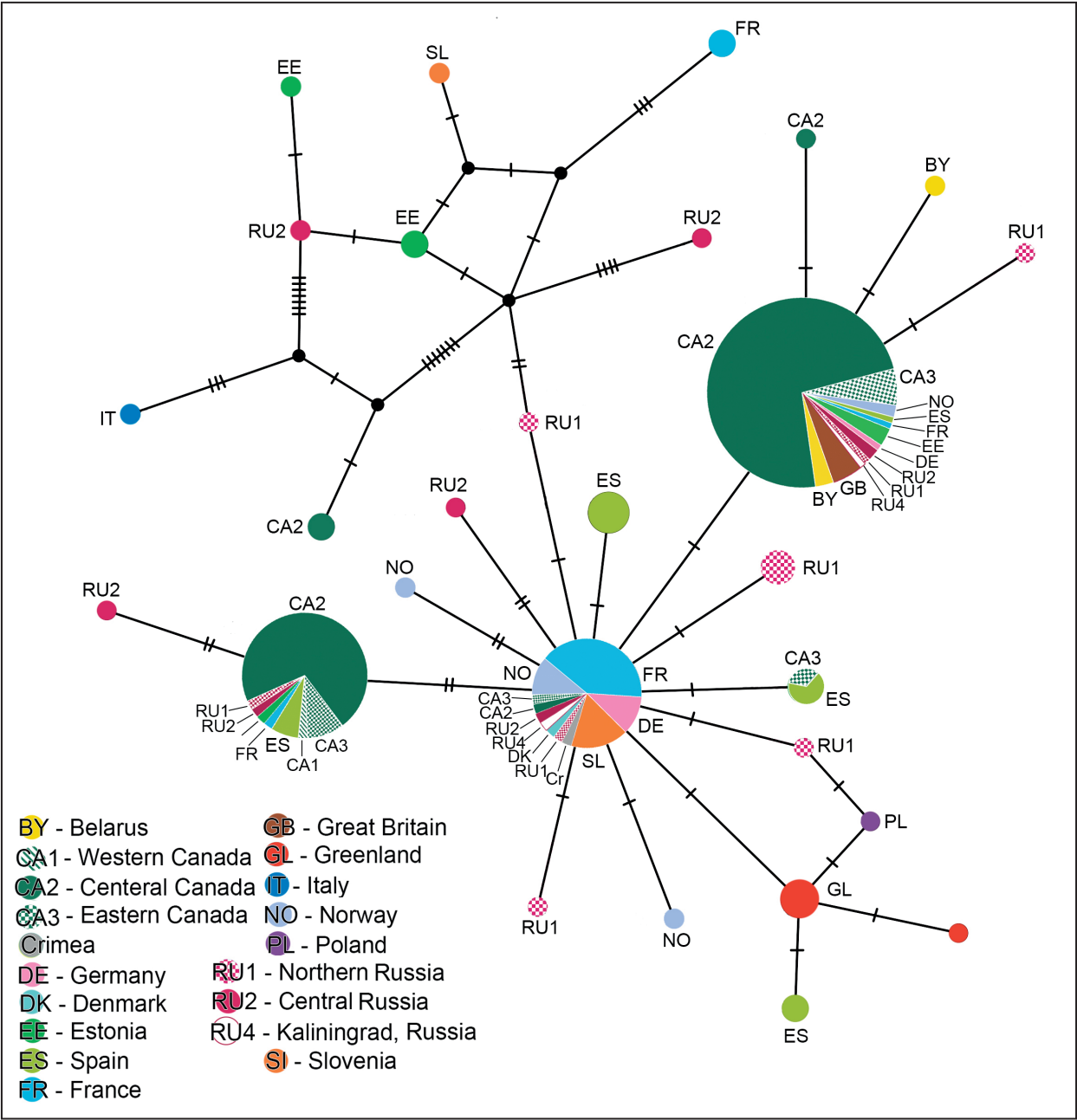


Figure 2. Haplotype network of *P. notabilis* lineage L2 based on 214 COI gene sequences (438 bp) obtained from 19 locations. Haplotype size is proportional to frequency. The number of transverse lines corresponds to mutational steps.

(8 and 7, respectively) compared to the more extensively sampled regions of central Canada and France (6 and 4 haplotypes, respectively).

Tajima's neutrality test revealed significantly negative values for Western Eurasia specifically, but not in North America (Table 3).

Table 3. Tajima's D index values

Lineage	Western Eurasia	North America
L1	-2.24 **	-0.93 ns
L2	-1.79 *	-1.25 ns

* P < 0.05, ** P < 0.01

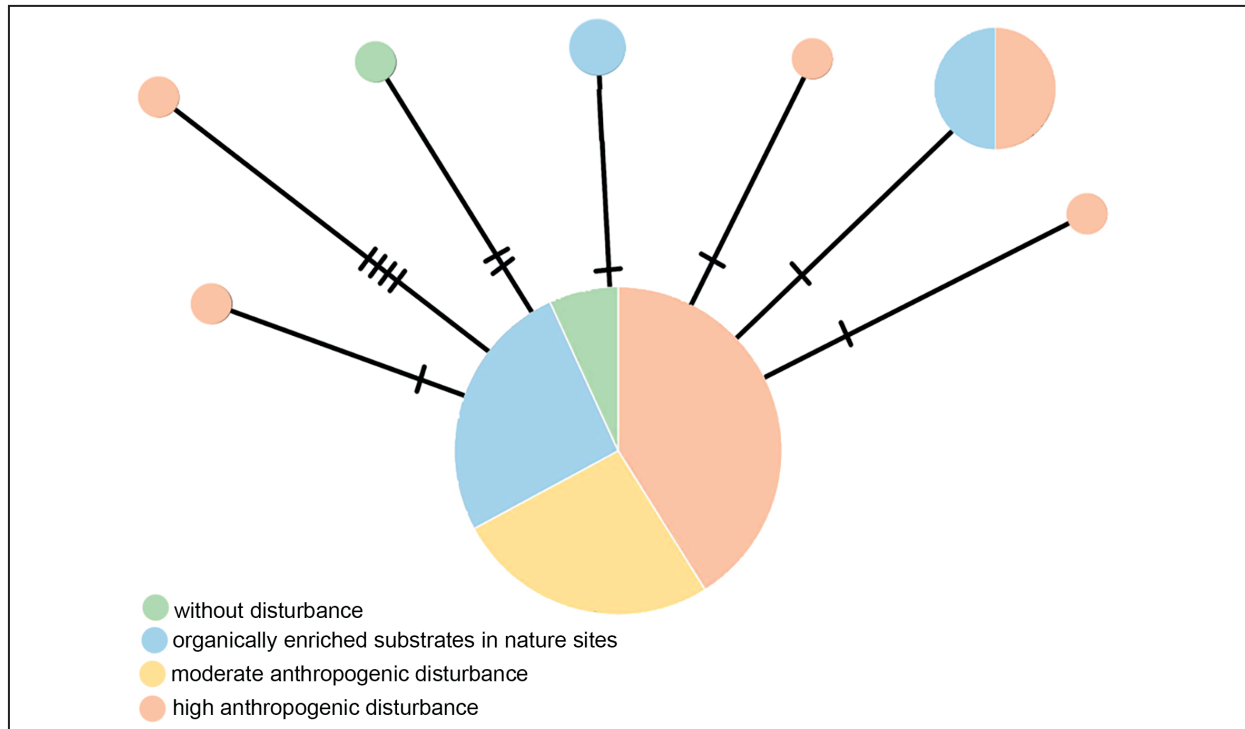


Figure 3. Haplotype network of *P. notabilis* lineage L1 based on 90 COI gene sequences (462 bp) from four habitat types. Haplotype size is proportional to frequency. The number of transverse lines corresponds to mutational steps.

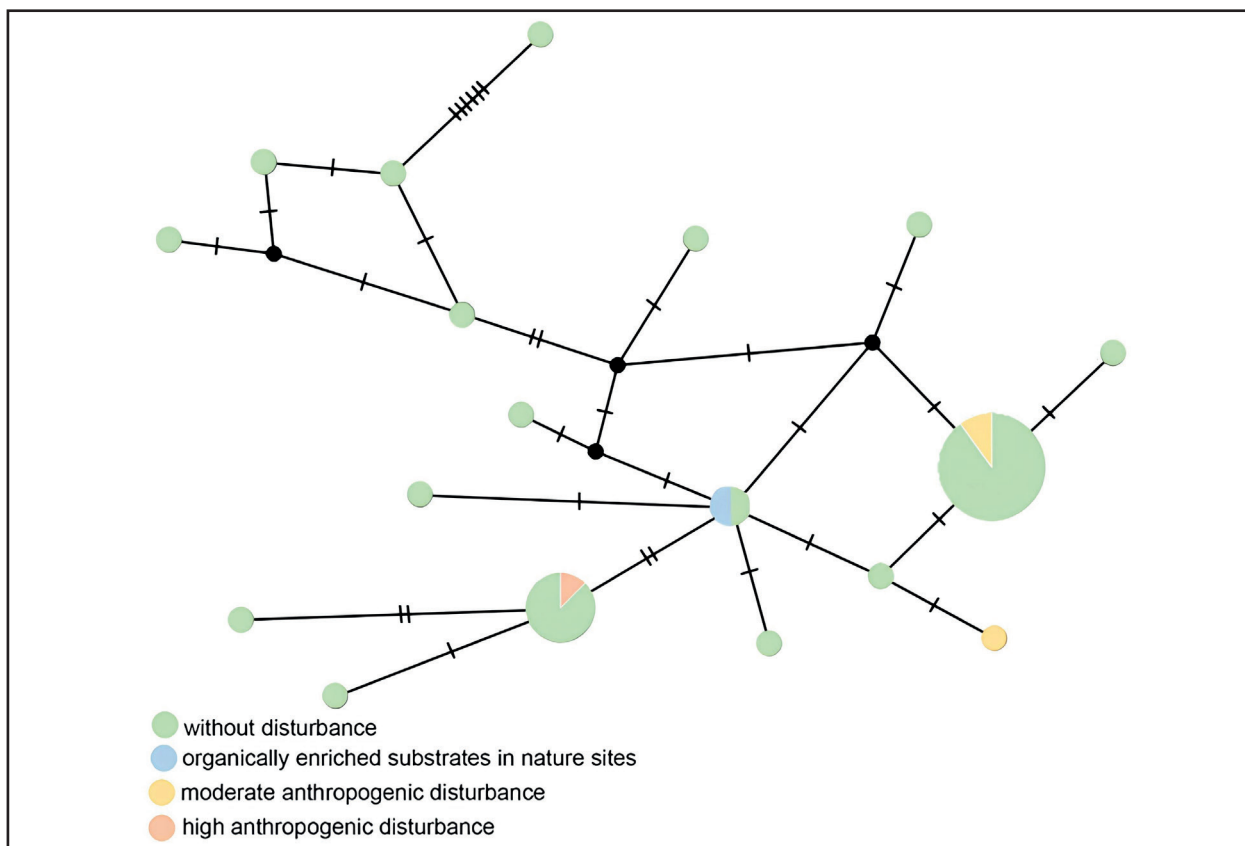


Figure 4. Haplotype network of *P. notabilis* lineage L2 based on 45 COI gene sequences (438 bp) from four habitat types. Haplotype size is proportional to frequency. The number of transverse lines corresponds to mutational steps.

Habitat association

For genetic lineage L1, no apparent associations were observed between specific haplotypes and particular habitat types (Fig. 3). The majority of examined individuals, regardless of haplotype, were associated with disturbed habitats: high anthropogenic disturbance (43%), moderate anthropogenic disturbance (21%), and organically-enriched substrates in natural sites (29%). Only 7% of specimens were found in undisturbed habitats. The most prevalent haplotype occurred across all habitat types but showed clear preference for disturbed environments.

In contrast, nearly all local haplotypes of genetic lineage L2 were found exclusively in undisturbed forests, with only a single haplotype occurring in a forest park (Fig. 4). The three most prevalent haplotypes consisted predominantly of individuals from undisturbed forests, with only a minor proportion originating from disturbed habitats.

4 Discussion

Genetic diversity provides insights into the origin and dispersal of taxa (Avise, 1989). The springtail genus *Parisotoma* shows notable diversity in two regions, southern Africa and eastern Asia (Potapov, 2001). While it remains uncertain in which region this genus first arose, African species exhibit greater morphological diversity (Janion-Scheepers et al. 2023), suggesting a more probable African origin. The cosmopolitan *P. notabilis* also occurs in South Africa, though it is particularly abundant and genetically diverse in Western Eurasia, especially in the Caucasus region where we have identified 10 of the 12 currently known lineages (Striuchkova et al. 2024). The species may have originated within this region, though definitive conclusions are not yet possible given the limited available data on *P. notabilis* genetic lineages in eastern Asia. In North America, only widespread lineages (L0, L1, L2, L4-Hebert) have been reported, with no endemic lineages yet discovered.

Saltzweid et al. (2017) suggested that the divergence of the L2-L1-L0 clade from other lineages occurred during the Miocene (11.5 million years ago). This group underwent further divergence to generate lineage L2 9.4 million years ago, while lineages L0 and L1 diverged 7.4 million years ago. A more recent phylogenetic tree (Striuchkova et al. 2024) comprising 11 lineages identifies the same clade, which now includes the recently described Iranian lineage L-Hyrcan (Lafooraki et al. 2022). The inclusion of this Iranian lineage, which is most closely related to L1, suggests a potential origin of this lineage

group in the Caucasus region. However, lineage L2 has not yet been found in this region. The L2-L0-L-Hyrcan-L1 clade is not the most ancient in the *P. notabilis* phylogeny, and among the lineages of interest, L1 is younger than L2. In contrast to the findings of Saltzweid et al. (2017), our COI gene data do not show a division of lineage L1 into two sub-lineages (Fig. 1). We accept that this may be an artifact of using a shorter fragment (438–462 bp) in this study than von Saltzweid et al. (2017) (709 bp). However, in a separate study using a longer fragment (658 bp) we also did not find sub-lineages (Striuchkova et al. 2024).

Despite relatively intensive genetic studies of this species in North America (Canada), haplotype diversity of both L1 and L2 lineages remains substantially lower than in Western Eurasia, further supporting their Palearctic origin. In North America, few haplotypes were found that do not occur in Western Eurasia: only 2 of 11 known haplotypes in lineage L1 and 3 of 28 in lineage L2. This further supports the allochthonous nature of the L1 and L2 lineages in North America. These lineages likely colonized North America from East Asia, potentially via the Bering land bridge that connected the continents multiple times during the Pleistocene over the last 3 million years (Hopkins, 1967). However, more data from East Asia are required to confirm this. The low number of autochthonous haplotypes for both lineages in North America, coupled with their very low similarity to Western Eurasian ($J = 13\text{--}14\%$), indicates that only a limited haplotype diversity initially reached North America, suggesting a relatively later colonization history compared to Eurasia. Tajima's *D* test values for both lineages show no significant deviations from zero in North America, indicating neutral population development as these lineages gradually integrated into local collembolan communities without undergoing population bottlenecks or expansion events.

The two most widespread lineages of *P. notabilis* (L1 and L2) differ in multiple aspects. These differences are most strikingly reflected in their haplotype networks. The “star-like” pattern observed in lineage L1 is characteristic of species that have undergone relatively recent and rapid expansion (Ferrerri et al. 2011), a suggestion further supported by significantly negative Tajima's *D* values in Western Eurasia (Table 3). Saltzweid et al. (2017) suggested that this is due to the species' tolerance to anthropogenic disturbance. However, our data show that this tolerance is not characteristic of the species as a whole, but only of the L1 lineage (Striuchkova et al. 2022). Moreover, the current study reveals that the range expansion of lineage L1 is associated with a single, clearly dominant haplotype (Fig. 1), which we designate as L1 α .

“Star-like” haplotype networks have also been documented in other microarthropod species, such as the

oribatid mite *Pantelozetes paolii* – also a eurytopic and abundant species with Holarctic distribution (Kokořová et al. 2021). At the species level (rather than lineage level), such “star-like” haplotype networks have been demonstrated in the Antarctic springtails, *Folsomotoma octooculata* and *Friesea antarctica* (Carapelli et al. 2017; Greenslade, 2018). In all these cases, the authors suggested relatively recent expansion events for both lineages and species.

Lineage L2 exhibited a distinct “web-like” haplotype network structure. This pattern, combined with weakly negative Tajima's D values in Western Eurasia, indicates slower spatial expansion compared to the lineage L1. The substantially higher haplotype diversity in L2 (28 vs 11 in L1) aligns with its more ancient origin, having diverged 2 million years earlier than L1 (Saltzweid et al. 2017; fig. 2).

The differences between the lineages are clearly reflected in the haplotype networks constructed according to their occurrence in different habitat groups varying in disturbance levels: natural habitats – organically enriched substrates in natural sites – moderate anthropogenic disturbance – high anthropogenic disturbance (Fig. 4). The category “organically enriched substrates in natural sites” was established to address the hypothesis of which sites originally gave rise to lineage L1, which now successfully colonizes anthropogenic environments. We hypothesized that L1 originated in more ephemeral habitats with temporary accumulations of organic matter. Such environments in nature are typically associated with localized disturbances, including river floodplains and decomposing fallen timber in forests. *Parisotoma notabilis* has been consistently documented in floodplain habitats (e.g., Russell et al. 2004), with experimental studies demonstrating its tolerance to several days of flooding (Nefedieva & Kuznetsova, 2023). Similarly, this species has been recorded in substantial numbers during the early stages of wood decomposition stages (Bokova, 2000). We collected samples from river flood deposits and decaying wood, where we identified lineage L1 of *P. notabilis* based on 28S rRNA gene analysis. However, these data were not incorporated into the haplotype network here as it was constructed exclusively using COI mitochondrial sequences. Indeed, over 90% of L1 individuals were found in disturbed habitats, with 29% specifically occurring in “organically enriched substrates in natural sites”. Thus, the successful colonization of anthropogenic habitats by this lineage was probably the result of already existing adaptations associated with the development of an ephemeral local resource. Such an ecological strategy is fundamentally linked to r-selection, which favors reduced generation times and increased reproductive output. (MacArthur & Wilson, 1967). In separate laboratory experiments, we have demonstrated that lineage L1 differs from L2 with, on average, 33% shorter egg development

time and possession of characteristics of ruderal species such as enhanced tolerance to heavy metals, desiccation and thermal stress (Striuchkova et al. in press).

Lineage L1, which is almost exclusively associated with disturbed habitats, can be termed “anthropogenically-associated”. In contrast, lineage L2 is found nearly exclusively in natural forests (Fig. 4). Both these lineages, along with L4-Hebert, coexist in moderately disturbed habitats such as urban forest parks (Striuchkova et al. 2022). This indicates they belong to the same *P. notabilis* s.l. population. Consequently, the previously documented different responses of this species' populations to anthropogenic factors (Fountain & Hopkin, 2004; Salamon & Alphe, 2009) are likely determined by varying proportions of these genetic lineages within *P. notabilis* s.l. populations.

5 Conclusions

Our study highlights the importance of an integrated ecological-geographical approach to understanding cryptic diversity. *Parisotoma notabilis* comprises genetically distinct lineages exhibiting levels of divergence that reach interspecific levels. Widespread lineages display distinct spatial patterns: a “star-like” structure for L1 and a “web-like” pattern for L2. These lineages colonize different habitat types, with L1 dominating disturbed habitats, while L2 prevails in natural forests and meadows. Of particular interest are L1's adaptations to anthropogenic habitats. This lineage likely originated from colonization of organic-rich but ephemeral natural substrates. We hypothesize that individuals adapted to elevated temperatures, desiccation, and frequent exposure to pollution had higher survival in such substrates. These traits – combined with an r-strategy (Striuchkova et al. in press) – enabled L1 to successfully colonize anthropogenically-disturbed habitats. This adaptive suite evolved within a single dominant haplotype, L1a. Our data highlight that genetic studies of Collembola require sampling from both natural and anthropogenic habitats. Ecological speciation appears equally relevant in parthenogenetic species as in bisexual ones. Moreover, consolidation and spread of these adaptations may also involve rare sexual reproduction, as males occasionally occur in this species (Potapov, 2001). Emerging research on other springtail species (e.g., Fedičová et al. 2025) now enables broader evaluation of this phenomenon's prevalence.

Our results highlight mechanisms underlying species' adaptation to anthropogenic environmental change, potentially facilitating transcontinental colonization.

Specific genetic variants may determine ecological resilience in human-altered ecosystems. These findings underscore the critical need to incorporate cryptic diversity assessments when evaluating anthropogenic impacts on soil communities.

Acknowledgements

This work was supported by the Russian Science Foundation grant number 22-24-00984. We are deeply grateful to Mikhail Potapov for his valuable consultations and expert advice and Peter Convey for advising on the text and language use. We also sincerely thank Cheng-Wang Huang for kindly providing the sequence data from China.

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Appendix 1. GenBank accession numbers

Lineage L1:

HM909156, GU656217, GQ373667, GQ373668, GU656408–GU656411, GU656418–GU656423, GU656430–GU656433, HM397729, HM397803, HQ559271, HQ942514, HQ942680–HQ942685, JN298124–JN298134, JQ935037–JQ935040, JQ935042–JQ935055, JQ935057–JQ935061, JQ935070, JQ935076–JQ935082, JQ935086, JQ935089, JQ935090, JQ935093–JQ935100, JQ935102–JQ935107, JQ935109–JQ935127, JQ935129–JQ935148, JQ935150–JQ935152, JX008093, JX008097, JX008098, KJ792225–KJ792229, KJ792238, KJ792244–KJ792253, KJ792263–KJ792267, KJ792287–KJ792290, KJ792304–KJ792308, KJ792319–KJ792323, KJ792335–KJ792344, KT704361, MF603399, MF603710, MF604171, MF604837, MF606397, MF606768, MF607407, MF607873, MF608273, MF608290, MF609583, MF609938, MF610472, MF610667, MF610721,

Lineage L2:

JQ935186, GQ373669, GQ373670, HG422622–HG422624, HM398181, JN298119–JN298123, JQ935155, JQ935160–JQ935162, JQ935165–JQ935171, JQ935173, JQ935175, JQ935176, JQ935178–JQ935180, JQ935183–JQ935185, JQ935188–JQ935190, KJ792237, KJ792240–KJ792243, KJ792254, KJ792263–KJ792267, KJ792277–KJ792281, KJ792291–KJ792303, KJ792314–KJ792318, KJ792324–KJ792334, KT703403, KT704739, KT708595, LK024502–LK024504, MF603100, MF603969, MF603986, MF604064, MF604092, MF604171, MF605501, MF605932, MF606658, MF607048, MF607069, MF607458, MF607604, MF608240, MF609473, MF609625, MF609837, MF609976, MF610205, MF610311, MF611357, MG031438, MG031560, MG031618, MG031701, MG031786, MG031880, MG031984, MG032087, MG032170, MG032183, MG032246, MG032395, MG032561, MG032598, MG032626, MG032692, MG032772, MG033087, MG033159, MG033224, MG033234, MG033541, MG033619,

MG033746, MG033771, MG033824, MG033978, MG038225, MG038272, MG038427, MG038506, MG034060, MG034133, MG034213, MG034318, MG038568, MG038711, MG038812, MG038814, MG034414, MG034487, MG034518, MG034576, MG038867, MG039013, MG039193, MG039604, MG034694, MG034698, MG034755, MG034764, MG039640, MG039703, MG039860, MG039916, MG034848, MG035198, MG035278, MG035302, MG040077, MG040113, MG040269, MG040281, MG035326, MG035389, MG035396, MG035400, MG040519, MG040717, MG040720, MG041081, MG035519, MG035606, MG035730, MG035943, MG041204, MG041239, MG041324, MG041343, MG036347, MG036348, MG036470, MG036609, OP861657–OP861659, PP235114, PP235116–PP235119, MG036712, MG036924, MG037023, MG037285, PP235126, PP235147–PP235151, PP235208–PP235212, MG037308, MG037316, MG037325, MG037534, PP235216, MG037693, MG037879, MG038165, MG038215,