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1 **Move or change, an eco-evolutionary dilemma: the case of Collembola**

2 Jean-François Ponge*

3

4 **Abstract**

5 The present opinion paper suggests that springtails, which can live above- and/or belowground
6 according to species requirements, have two strategies at their disposal to face environmental hazards,
7 called ‘move’ or ‘change’. Species with poor dispersal capacity, often parthenogenetic, and living
8 mainly in a confined environment, have to adapt themselves by increasing their phenotypic plasticity
9 or letting the environment selecting or adding favourable mutations. Conversely, species with a high
10 dispersal capacity, often sexual and living in a more open environment, may emigrate and immigrate
11 without the need to become better adapted to changing environmental conditions. Advantages and
12 disadvantages of these two tactics are reviewed and their prospective responses to global changes are
13 compared on the light of existing knowledge on this microarthropod group.

14 **Keywords**

15 Collembola Movement Dispersal Adaptation Evolution Strategy

16 **Introduction**

17 It may seem at first sight surprising that some living forms crossed geological ages without any
18 pronounced changes in their appearance while others diverged to a great extent (Gould and Eldredge
19 1993). Examples of the former are ‘living fossils’, as the coelacanth (Amemiya et al. 2013) and the
20 wollemi pine (McLoughlin and Vajda 2005). Both of them are still living in stable and concealed
21 marine and terrestrial environments, respectively, which offered them some unexpected protection
22 until they became endangered in their original niches by the ineluctable growing impact of human
23 activities in the Anthropocene (Dirzo et al. 2014). Let us highlight the case of springtails
24 (Collembola), known from the Early Devonian, ca. 400 Ma ago (Scourfield 1940, Greenslade and
25 Whalley 1986), and present in terrestrial environments as diverse, modern species assemblages as
26 soon as the Early Cretaceous, ca. 110 Ma ago (Sánchez-García and Engel 2017, Sánchez-García et al.
27 2018). Palaeozoic families have seemingly crossed the Cretaceous-Paleogene (K-Pg) mass extinction,
28 which devastated the global environment and destroyed three quarters of plant and animal species on

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29 Earth ca. 66 Ma ago. Christiansen and Pike (2002) evoked a taxonomic turnover at genera level while
30 other authors support the idea that most present-day genera crossed the crisis (Richards 1968, Hädicke
31 et al. 2013). These tiny arthropods are worldwide spread and live in various environments as soil
32 (from litter to deep soil), vegetation (from lichen and moss carpets to tree crowns), ponds, salt
33 marshes, deserts, glaciers (Hopkin 1997). However, the species composition of their communities
34 differ at large-scale among continents and islands because of geographic isolation (Shaw et al. 2013),
35 and at small-scale among micro-habitats because of adaptive specialization (Salmon and Ponge 2012).
36 In heterogeneous landscapes under the influence of human activities a deficit of recolonization
37 (ecological debt) is known to affect species moving more slowly, pointing to the importance of
38 dispersal for the survival of collembolan species in a changing environment (Ponge et al. 2006). This
39 urges us to question the strategies by which Collembola survived past ecological crises: will they
40 allow them surviving (or not) the ongoing sixth mass extinction (Barnosky et al. 2011)? In an
41 appealing paper Berg et al. (2010) stressed the importance of a good knowledge of biotic interactions
42 and functional traits linked to adaptation and dispersal if we want to predict the fate of species in a
43 global change perspective. In a recent paper Thompson and Fronhofer (2019) showed that adaptation
44 and dispersal conflict in the ability of species to survive environmental threats, pointing to the
45 existence of two opposite strategies or tactics which species have to select in order to avoid
46 disappearance. Here we prefer to turn the famous adage ‘adapt or disperse’ to ‘move or change’
47 because the latter has a wider acceptance. Movement of individuals for escaping bad conditions and
48 reaching safe sites may occur at small scale without any necessary involvement in metacommunity
49 dynamics, the background of dispersal (Mouquet and Loreau 2003). Accordingly, change has a wider
50 acceptance than adaptation, because some basic textbooks still restrict the meaning of adaptation to the
51 selection of favourable genotypes (Williams 2019), while individuals may change in the course of
52 their life as a direct response to the environment (Colinet and Hoffmann 2012).

53 **Why and how to move?**

54 The active motility of collembolan species is highly variable, depending on whether animals are
55 adapted to subterranean or aerial life and whether they possess organs making them able to walk or
56 jump (Vanhee et al. 2017). By active movement they are able to select habitats within a circle of up to
57 200m, above which dispersal limitation is commonly observed at community level (Ponge and Salmon
58 2013). Exceptions are directional mass movements of surface-living Collembola, which have been
59 observed in a little number of hypogastrurid and isotomid species (Hågvar 2000). Above the spatial
60 threshold below which animals are able to wander by their own means in a heterogeneous
61 environment, dispersal becomes a stochastic process mediated by long-distance carriers, e.g. birds,
62 insects, wind, water (Hawes et al. 2008, Robin et al. 2019).

63 Springtails have to move for a variety of reasons, e.g. foraging (Chauvat et al. 2014), mating
64 (Hedlund et al. 1990), selection of favourable places for moulting and oviposition (Verhoef and
65 Nagelkerke 1977, Benoit et al. 2009), avoidance of predation (Salmon 2004), toxicity (Michelozzi et
66 al. 1997, Sjögren 1997), desiccation (Hayward et al. 2004), and more generally in search for more
67 favourable conditions (Salmon et al. 2002). Active movement can occur from millimetre to decimetre
68 scale, using chemical communication to detect food (Bengtsson et al. 1988, Salmon and Ponge 2001),
69 sexual partners (Waldorf 1974, Zizzari et al. 2017) or environmental threats such as those potentially
70 associated with dead conspecifics (Nilsson and Bengtsson 2004). Movement to places already
71 occupied by conspecifics, which are conditioned by aggregation pheromones (Salmon et al. 2019),
72 help to find safe sites for growth, reproduction and protection from natural enemies and environmental
73 hazards (Wertheim et al. 2005), tendency for aggregation increasing with the age of animals (Barra
74 and Christiansen 1975).

75 Small-scale movement may occur horizontally, for instance between adjacent patches of
76 litter/vegetation (Auclerc et al. 2009), or vertically, between or within soil and litter horizons (Hassall
77 et al. 1986, Sgardelis et al. 1993, Krab et al. 2010) or between vegetation and soil (Bowden et al.
78 1976). Vertical movement is favoured in soils having a network of earthworm galleries (Marinissen
79 and Bok 1988, Salmon 2004). Small-scale movement can be directional, using olfactory cues (Auclerc
80 et al. 2010) or non-directional, ceasing only when preferred habitat or food are randomly encountered
81 (Nilsson and Bengtsson 2004). At larger scale, movement may occur among several favourable
82 habitats distributed within a given landscape, colonization rate decreasing with distance (Hertzberg
83 1997, Ojala and Huhta 2001) and increasing with ancientness and quality of favoured habitats
84 (Heiniger et al. 2014). The capacity of movement increases with size, larger species (Sjögren 1997)
85 and adult stages (Johnson and Wellington 1983) moving to larger distances than smaller species and
86 juvenile stages, respectively. The existence of a functional jumping apparatus and long legs associated
87 with epigeic life (Salmon et al. 2014) still increases distances travelled (Chauvat et al. 2014).
88 Movement occurs individually (Bengtsson et al. 2004), increasing at high population density
89 (Bengtsson et al. 1994), or as mass movement at the surface of litter (Lyford 1975) or snow patches
90 (Hågvar 1995). At last, large-scale passive travel by air (Hawes et al. 2007) and water (Schuppenhauer
91 et al. 2019) has been recorded, and was shown or suspected to occur in the colonization of islands
92 (Moore 2002), glacier moraines (Flø and Hågvar 2013), open cast mining areas (Dunger et al. 2002),
93 mining refuse tips (Moore and Luxton 1986), tree canopies (Van der Wurff et al. 2003), or roofs
94 (Joimel et al. 2018).

95 **Why and how to change?**

96 In Collembola, adaptive changes were mostly deduced from comparisons among existent populations,
97 but recent developments in molecular biology allow or might allow to discern the mechanisms
98 involved in evolutionary change. Most fruitful studies concerned the adaptation of Collembola to
99 heavy metal toxicity. Duplication of the gene encoding metallothionein (MT, a sulphur-rich protein
100 complexing metals) is known for a long time to confer tolerance to heavy metals in natural populations
101 of *Drosophila melanogaster* (Maroni et al. 1987). This mechanism does not seem to occur in metal-
102 adapted populations of Collembola. In the species studied so far, *Orchesella cincta*, higher tolerance to
103 cadmium was suggested to result from differential transcriptional regulation and selection of more
104 efficient alleles at a single locus under metal stress (Janssens et al. 2009). However, a number of genes
105 have been shown to have expanded as gene clusters, i.e. groups of genes coding for the same protein,
106 some of them directly associated with metal stress tolerance, in the genome of *O. cincta* (Faddeeva-
107 Vakhrusheva et al. 2016). Horizontal gene transfer (HGT), either from bacteria or fungal origin, has
108 been also shown to have occurred repeatedly in the evolution of the genome of *O. cincta*, suggesting
109 that HGT could have also played a role in its adaptation to metal stress (Faddeeva-Vakhrusheva et al.
110 2016). More research is needed, on a wider array of species, before reaching conclusions about the
111 evolution of tolerance within Collembola. Epigenetic changes, such as those mediated by DNA
112 methylation, have been shown to contribute to tolerance of environmental hazards in vertebrates and
113 plants (Merritt and Bewick 2017), but have not been tested as yet in invertebrates.

114 It has been observed that sexual populations of the otherwise asexual (parthenogenetic)
115 *Mesaphorura macrochaeta* commonly occur in stressed environments (Niklasson et al. 2000, Gillet
116 and Ponge 2003). Sexual reproduction allows the selection of better-adapted combinations of alleles
117 (Hickey and Golding 2018), but the mechanism of this reproductive shift is still unknown. *Wolbachia*-
118 induced parthenogenesis is known to be the rule in *M. macrochaeta* (Czarnetzki and Tebbe 2003) but
119 the sexual population from a metal-polluted site studied by Gillet and Ponge (2003) was shown to be
120 cured of *Wolbachia* (Jacintha Ellers, personal communication), suggesting either (i) a detrimental
121 effect of heavy metals on symbiotic bacteria or (ii) the selection of metal-tolerant bisexual strains
122 within populations of *M. macrochaeta*. The adaptive (or maladaptive) value of *Wolbachia* infection
123 remains to be demonstrated in Collembola, while studies on *Drosophila* showed that *Wolbachia*
124 protect their host against pathogens (Martinez et al. 2014). Laboratory experiments by Chahartaghi et
125 al. (2009) demonstrated that parthenogenetic collembolan species were faster colonizers than sexual
126 species, supporting the classical hypothesis of parthenogenetic general purpose genotypes (Weider
127 1993) as having a wider geographical distribution (Lynch 1984). Alternative explanations have been
128 given for the appearance of high phenotypic plasticity within species lineages, such as among others
129 the accumulation of clonal diversity within asexual populations (Pound et al. 2004) or the inheritance

130 of epigenetic modifications (e.g. DNA-methylation) under variable environmental conditions
131 (Massicotte and Angers 2012).

132 Non-adaptive changes also exist (Czekanski-Moir and Rundell 2019). They may result from
133 allopatric speciation, i.e. genetic drift following the establishment of a few founder individuals in an
134 environment identical from the area of origin but remote from it (Templeton 1980) or after the
135 appearance of a geographic barrier to gene flow, e.g. by fragmentation, within the original area
136 (Cracraft 1982). Geographic speciation has been shown to occur among cave Collembola (Katz et al.
137 2018) and both dispersal- and vicariance-driven processes have been demonstrated by phylogenetic
138 analysis in Antarctic springtails (McGaughran et al. 2010). However, non-geographic barriers (e.g.
139 reproductive isolation) also exist, reducing gene flow within populations, and thus favouring the
140 appearance of new species by sympatric or parapatric speciation (Bird et al. 2012). For instance
141 mutations may result in sexual isolation (Kaneshiro 1980) or habitat specialization (Kawecki 1997).
142 Sexual selection in Collembola can be traced from the choice exerted by females for spermatophores
143 produced by some males against others (Gols et al. 2004), with a preference for those of closely
144 related conspecifics (Hedlund et al. 1990). Chemical communication plays a prominent role in
145 collembolan mating, indirect sperm transfer and associated behaviour (Porco et al. 2004, Zizzari et al.
146 2017). The appearance of avoidance behaviour or even just the lack of chemical recognition among
147 conspecifics may also allow animals from the same original population to segregate in space or time
148 (Haim and Rozenfeld 1993, Guo et al. 2012). In Collembola, the checkerboard distribution of sibling
149 species with similar ecological requirements, like the widely distributed Holarctic sexual isotomids
150 *Folsomia quadrioculata* and *Folsomia manolachei* (Ponge and Salmon 2013), could be explained by
151 non-adaptive speciation mediated by behavioural divergence (Pillay and Rymer 2012).

152 **Move and change: vicariant or additive strategies?**

153 In stable environments (Levins 1962), periodic changes (e.g. seasons) or slow changes occurring along
154 decades (e.g. vegetation dynamics) allow animals to adapt their cycle (Takeda 1987). In the presence
155 of small-scale heterogeneity animals can move from one habitat to another (Loranger et al. 2001)
156 without the need to adapt themselves to novel conditions, and the same when recolonizing at short
157 distance after a disturbance (Alvarez et al. 2000, Auclerc et al. 2009). When the environment changes
158 suddenly and that above habitat requirements (e.g. following abrupt land use change), any given
159 population, to ensure its survival, has to strike a balance between long-distance dispersal to more
160 favourable habitats, or rapid adaptation (Pease et al. 1989). But what are the respective advantages and
161 disadvantages of dispersal and adaptation? The answer relies on interactions between species traits and
162 environmental features (Berg et al. 2010). Long-distance dispersal may occur by inter-patch
163 movement within a landscape, following a 'stepping-stone' model (Kimura and Weiss 1964), with a

164 strong discrepancy in successful establishment between species according to their tolerance to hostile
165 matrices (Coulson et al. 2002). A high rate of mortality is expected in specialists, when forced to
166 abandon their favoured habitat, while generalists are not endangered, at least in the short term
167 (Heiniger et al. 2015). It has been shown on a wide array of plant and animal taxonomic groups that
168 specialists may become generalists in a relatively short amount of time (Colles et al. 2009). Horizontal
169 transfer of favourable genes (Faddeeva-Vakhrusheva et al. 2016), infection by *Wolbachia*
170 (Timmermans et al. 2004), or epigenetic processes (Zizzari and Ellers 2014, Szabó et al. 2019) may
171 contribute to such rapid adaptive changes in otherwise endangered species, but these events are rare
172 and there is a high risk of species disappearance in the meantime, at least locally, stemming in
173 ecological debt (Heiniger et al. 2014).

174 Let us take two examples showing that strongly divergent ecological groups of Collembola
175 have adopted different combinations of ‘move’ and ‘change’ as efficient strategies face to
176 environmental change.

177 Among epigeic species, *Orchesella cincta* is known to live in forest litter (Van Straalen et al.
178 1987), but this species is also able to live in moss, lichen and algal covers on tree trunks (Prinzing
179 2001, Shaw 2015) and in canopy-suspended soils (Shaw 2013). Genetic studies have shown that
180 distances of several kilometres do not limit gene flow (Fрати et al. 1992, Van der Wurff et al. 2003,
181 2005), genetic isolation occurring only at continental scale (Timmermans et al. 2005). Given that all
182 populations exhibit a high allelic diversity (Timmermans et al. 2007, Janssens et al. 2007, 2008), it
183 ensures that gene flow between remote populations is enough to ensure genetic mixing. This species
184 most probably combines active movement within woody patches and transport by wind between
185 patches, even remote ones when climbing on tree trunks and canopies (Prinzing and Wirtz 1997, Shaw
186 2015). The high allele variety (favoured by intense exchanges within sexual metapopulations) allows it
187 to rapidly adapt to environmental hazards by allele recombination or selection of most efficient ones
188 (Janssens et al. 2007, 2008, Bahrndorff et al. 2010). Thus the strategy adopted by *O. cincta* face to
189 environmental hazards combines a high genetic diversity (based on genetic admixture and sexual
190 reproduction) with active movement and long-distance passive dispersal among distant populations.

191 Among endogeic species, *Folsomia candida* is known to avoid light (Fox et al. 2007, Gallardo
192 Ruiz et al. 2017), living in a subterranean space where movement is limited to the search for microbial
193 food (Klironomos et al. 1999, Auclerc et al. 2010). Being parthenogenetic from *Wolbachia* infection
194 (Vandekerckhove et al. 1999, Pike and Kingcombe 2009), there is no need to move for searching
195 conspecifics, and reproduction occurs at a high rate in the absence of overcrowding (Green 1964),
196 making the species able to colonize rapidly a novel environment (Dunger et al. 2002), starting from
197 even a single female, like most laboratory strains were started (Fountain and Hopkin 2005). The

198 existence of general-purpose genotypes has not been demonstrated in *F. candida*, but studies done as
199 yet suggest that this species has adopted a strategy of high plasticity with extensive gene expression
200 regulation (De Boer et al. 2011). *F. candida* is able to cope with nutrient scarcity (Hafer et al. 2011),
201 drought and cold (Bayley et al. 2001), elevated carbon dioxide concentration (Jones et al. 1998) and
202 pollution (Crommentuijn et al. 1995), with transgenerational transmission of acquired tolerance (Hafer
203 et al. 2011). Mutations are probably not rare, given the high rate of successive reproductive waves
204 from one individual (Fountain and Hopkin 2005). Despite the overall tolerance of the species,
205 substantial variation exists among clones (Crommentuijn et al. 1995) and between individuals of the
206 same clone (Crouau and Cazes 2003). Phylogenetic investigations showed that numerous strains exist,
207 with two major clades derived from a unique ancestor (Tully et al. 2006), with small but clearly
208 recognizable morphological differences among strains (Tully and Potapov 2015), each strain having
209 its own reaction norms (Barateiro Diogo et al. 2007) and life-history traits (Mallard et al. 2015). A
210 high rate of horizontal transfer, among the highest found in metazoan genomes, has been reported in
211 the genome of *F. candida* (Faddeeva-Vakhrusheva et al. 2017).

212 Many other endogeic springtails share similar properties with *F. candida*, although they have
213 not been studied in such detail. In particular, ‘species’ of the mostly parthenogenetic genus
214 *Mesaphorura* exhibit strong morphological resemblances, justifying they were previously grouped in
215 the unique species *Tullbergia krausbaueri* (Gisin 1960), later erected to genus level as *Mesaphorura*
216 (Rusek 1971). The chaetotaxy, stable along several generations issued from a single specimen (Ponge,
217 personal observations), allowed the recognition of a huge and still increasing number of ‘species’
218 which may differ only by the presence or absence of a single pair of minute hairs on the integument. It
219 has been shown that at least some of these ‘species’ differ in their ecological preferences (Dunger
220 1991, Ponge 1993) and their molecular patterns (Zimdars and Dunger 2000), despite the fact that
221 several *Mesaphorura* ‘species’ commonly live together in the same soil volume (Ponge, personal
222 observations). This suggests that they do not differ in their taxonomic status from the various strains of
223 *F. candida*. Similar to *F. candida*, *Mesaphorura* species have a high reproductive rate, hence their use
224 as laboratory test animals (Boitaud et al. 2006, Sechi et al. 2014), but unfortunately their tolerance to
225 stress factors has not been studied yet, making further comparisons impossible. We only know that
226 sexual populations of the most common species, *M. macrochaeta*, are present in stressed
227 environments. This could mean that sexual reproduction occurs as an alternative to parthenogenesis
228 only in extreme environments. The strategy adopted by *F. candida* (and most probably other
229 *Wolbachia*-infected parthenogenetic springtails) is thus based on a high genetic diversity, with the
230 rapid occurrence of mutations (linked to high reproductive rates), combined with a high phenotypic
231 plasticity, general-purpose genotypes remaining to be discovered, but being highly probable. Large-
232 scale movement does not take place in this strategy.

233 These two cases are extreme cases, exemplifying opposite strategies adopted by belowground
 234 versus aboveground species (Van Dooremalen et al. 2013). It is highly probable that many species, in
 235 particular species living in litter, the so-called ‘hemiedaphic’ ecological group (Nickerl et al. 2013),
 236 combine movement and change (whether genetic or phenotypic, whether based on mutation or
 237 recombination) to ensure their survival (Fig. 1). The two above cited model species, *F. candida* and *O.*
 238 *cincta*, displaying opposite strategies of move and change, have been positioned at lower and upper
 239 sides of Siepel’s scaling of life cycles in microarthropods (Siepel 1994), respectively. However, most
 240 collembolan species, and in particular those living in litter, are midway along this scale of increasing
 241 juvenile stage duration and decreasing clutch size which follows the classical r-K selection gradient
 242 (Pianka 1970). Awaiting further research on collembolan life-history traits it can be hypothesized that
 243 trade-offs exist between the cost of move (Bonte et al. 2012) and the cost of change (Kawecki 1994).

244 We may now ask whether the hypothesis of two alternative strategies, here called ‘move’ and
 245 ‘change’ can be falsified. In other terms, are ‘move’ species able to adapt to changing conditions
 246 without resorting to movement. And, conversely, are ‘change’ species able to move to better habitats?
 247 Examples can be found in the above cited species. The overexpression of genes coding for
 248 metallothionein in populations of *Orchesella cincta* from metal-contaminated areas (Roelofs et al.
 249 2009), most probably of epigenetic origin (Janssens et al. 2009, Boyko and Kovalchuk 2011), indicate
 250 the capacity of a ‘move’ species to rapidly adapt to environmental stress. Dunger et al. (2002) showed
 251 that *Mesaphorura* spp. and *Folsomia candida* were early colonizers of open-cast mine areas, together
 252 with wind-transported epigeic springtails. This suggests that ‘change’ species can travel long distances
 253 with other means of dispersal than wind. Bird geophagy (Downs et al. 2019) and the well-known
 254 adhesion of earth to bird legs and beaks (Darwin 1859) can be suggested as potential mechanisms for
 255 this still poorly studied phenomenon of long-distance travel of edaphic species. Awaiting more
 256 research on this topic these two examples show that ‘move’ and ‘change’ strategies can be additive
 257 rather than mutually exclusive.

258 **‘Move’ or ‘change’ as a response to global change: which perspectives?**

259 Collembolan species with functional traits giving them a higher dispersal capacity (e.g. large body
 260 size, long furcula and legs, fully developed visual organs), here called ‘move’ species, are resistant to
 261 small-scale temporary disturbances, being able to recolonize easily after e.g. fire (Malmström 2012) or
 262 in the course of cultural cycles (Alvarez et al. 2000). However, in the case of cyclic, predictable
 263 disturbances occurring in natural and agricultural habitats, other strategies, such as changes in vertical
 264 distribution (Hassall et al. 1986) or survival as dormant eggs (Leinaas and Bleken 1983, Tamm 1986),
 265 are also observed. But what happens and will happen in the case of long-standing changes, such as
 266 present-day climate warming? In a 16-yr warming field experiment where subarctic Collembola were

267 able to migrate in and out of open top chambers, species having traits associated with the ‘move’
268 strategy did not follow the overall decrease in abundance and species richness associated with higher
269 temperature and lower moisture (Makkonen et al. 2011). However, straightforward advantages of
270 ‘move’ species, observed in subarctic collembolan communities in the frame of climate warming, were
271 not supported by other studies on communities from milder climates. For instance Yin et al. (2019)
272 showed that climate change had a negligible impact on collembolan communities compared to land
273 use change, although there was a strong interaction between land use and sensitivity to climate. By
274 sampling Collembola over several years widely differing in climate conditions, Pollierer and Scheu
275 (2017) showed that ‘change’ (parthenogenetic) species were sensitive to climate variation while
276 ‘move’ (sexual) species were not. While more studies based on functional traits are awaited, ‘move’
277 species can be thought at first sight better able to cope with rapidly changing environments than
278 ‘change’ species, given their ability to move to distant, favourable habitats (Ponge et al. 2006).
279 However we may ask whether there are limits to this adaptive behaviour in the frame of present-day
280 climate warming. In other terms, can dispersal limitation affect ‘move’ species if warming occurs at a
281 too high rate? Given that a 100m altitudinal gradient translates in a 100km latitudinal gradient in terms
282 of temperature variation (Jump et al. 2009), then a thousand times more time will be required along
283 latitudinal versus altitudinal gradients to track shifts in suitable climate (Schloss et al. 2012). This
284 rough calculation points to extinction risks for ‘move’ species if they rely only on this strategy for
285 their survival, to the exception of mountains which may play the role of less distant refuges if locally
286 present (Wright et al. 2009).

287 It can be hypothesized that in face of present-day climate change, inherently associated with
288 high land use turnover (Ojima et al. 1994), ‘change’ species with low dispersal rate will be threatened
289 compared to “move’ species, at least locally and temporarily if they have a wide distribution area
290 (Ponge and Salmon 2013) or at worldwide scale and definitively if they are endemic and specialized
291 on rarefying habitats (Garrick et al. 2004). However, among ‘change’ species, those having a high
292 phenotypic plasticity are prone to escape this genetic bottleneck. Species such as *Mesaphorura*
293 *macrochaeta* have even been shown to thrive in disturbed environments where other species fail to
294 survive (Gillet and Ponge 2003).

295 As a conclusion, we showed that collembolan species have at their disposal two opposite
296 strategies to face environmental hazards, among them the ongoing sixth mass extinction. Whether
297 trade-offs exist between these strategies is still a matter of conjecture, given the scarcity of studies on
298 the evolution of functional traits associated with collembolan tolerance (Van Dooremalen et al. 2013,
299 Prinzing et al. 2014, Tully and Potapov 2015). We hope that the present opinion paper will stimulate
300 future studies on the evolutionary ecology of Collembola, on the model of those already engaged by
301 Berg et al. (2010) and Thompson and Fronhofer (2019).

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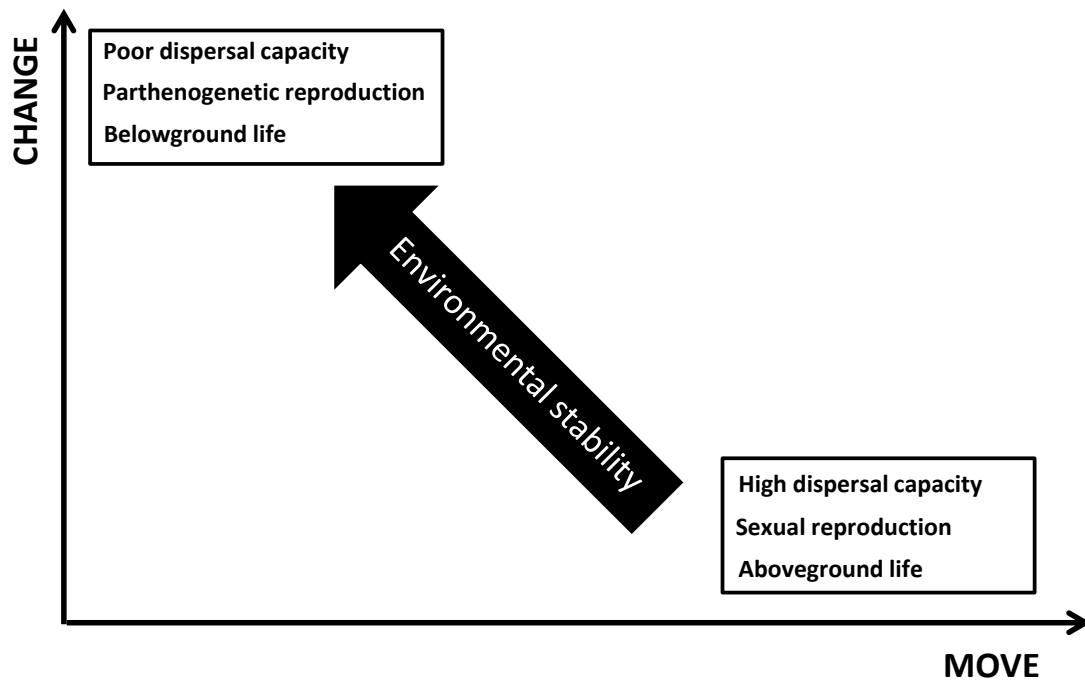
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737

738 **Fig. 1.** Sketch diagram showing main collembolan attributes linked to two opposite strategies face to
739 environmental hazards