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

Jean-François Ponge\*

## Abstract

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

## Keywords

Collembola Movement Dispersal Adaptation Evolution Strategy

## Introduction

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

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

### **Why and how to move?**

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

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

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

## **Why and how to change?**

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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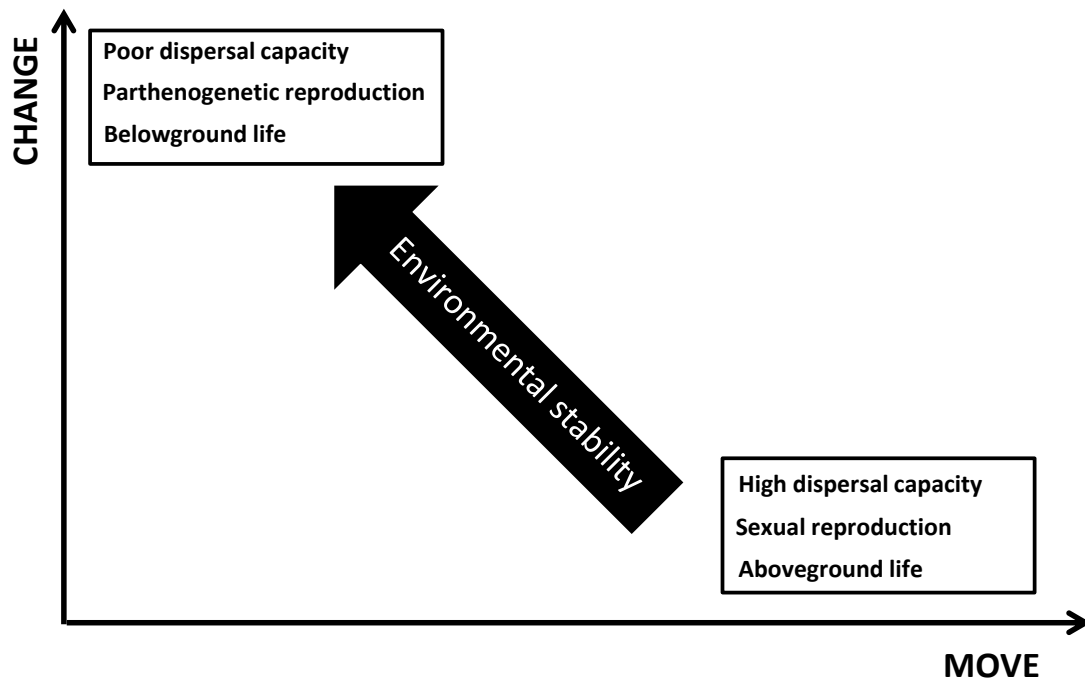
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738 **Fig. 1.** Sketch diagram showing main collembolan attributes linked to two opposite strategies face to  
 739 environmental hazards