

## Review

## Genetic structure of soil invertebrate populations: Collembolans, earthworms and isopods



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## ABSTRACT

Soil-living animals such as collembolans, earthworms and isopods are considered to be sedentary animals with only limited dispersal capacities. Therefore, gene flow among populations is expected to be low leading to significant population genetic differentiation due to random drift and local adaptation. We reviewed the literature to test this expectation. Our survey reveals a clear signature in the current pattern of genetic variation due to post-glacial colonization events. It also reveals that habitus can be a misleading predictor of dispersal capacity. In some species relatively high gene flow across considerable distances, most likely through passive dispersal (mediated by wind, water flow or animals), might counteract local genetic adaptation and will prevent loss of genetic variation.

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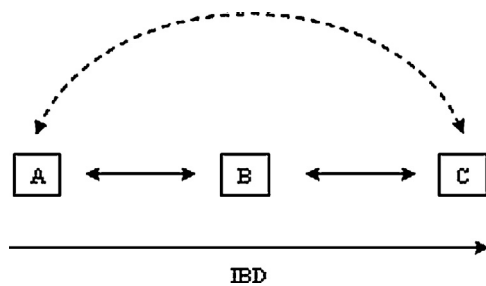
## 1. Introduction

Population genetic structure is the distribution of genotypes in space and time and is determined by both historical and current evolutionary processes (Hewitt and Butlin, 1997) involving gene flow, genetic drift and selection (Slatkin, 1987). The absence of migration among populations either due to the existence of barriers or due to limited dispersal abilities of individuals, will limit the rate of gene flow. Under such conditions allele frequencies in each population will be subject to independent random changes (Hartl

and Jones, 1998). Because populations have a finite size, only a subset of parental alleles is represented among the offspring, causing fluctuations of allele frequencies over generations and fixation of random alleles due to genetic drift. This may further increase genetic differentiation among populations (Hartl and Jones, 1998).

Without the homogenising effect of gene flow, genetic diversity will decrease over time, which might impair the capacity of populations to cope, among others, with novel environmental conditions; this may eventually lead to future local extinction if the conditions change (Burger and Lynch, 1995; Spielman et al., 2004). Genetic divergence of populations subject to different environmental conditions can also be influenced by selection. If local directional selection is strong enough, genetic differentiation can occur even in the presence of gene flow (Ehrlich and Raven, 1969). The

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**Fig. 1.** Scheme of the isolation-by-distance (IBD) process. The homogenizing effect of gene flow is due to short-range dispersal among adjacent populations as described by a stepping stone model of gene flow (full arrows). As a result an isolation-by-distance pattern may be observed, in which distant populations are more differentiated than closer ones. However, in situations where migration occurs mainly over long distances, populations far apart may become more similar to each other than populations in proximity (hatched arrows).

accumulation of genetic differences among populations can, however, be counteracted by dispersal (Slatkin, 1987). In fact, only a small number of individuals exchanging genetic material between populations (absolute number of migrants,  $N_m > 1$ ) is already sufficient to prevent the development of high levels of genetic differentiation (Slatkin, 1987; Wright, 1943). Dispersal of organisms is an important feature to understand their genetic and geographic distributions.

The geographic population structure resulting from drift and dispersal is often represented by the model of “isolation-by-distance”. Under this model a continuous increase of genetic distance between populations is expected with increasing geographic distance (Slatkin, 1985; Wright, 1943). Isolation-by-distance is supported by dispersal over small distances among neighbouring populations like in a stepping stone model of gene flow (Kimura, 1953) (Fig. 1). With this model the number of individuals that disperse per generation may be estimated using allele frequencies measured by allozymes, restriction site polymorphisms and DNA sequence data (Slatkin, 1987; Wright, 1943). Such indirectly derived estimates of dispersal are often considerably greater than direct measurements, which is usually interpreted to indicate that direct methods tend to greatly underestimate dispersal events (Koenig et al., 1996).

Current evolutionary processes act on a historical genetic background, determining the present population genetic structure (Hewitt and Butlin, 1997). Historical events, for example glaciations, are known to have had a major impact on the geographic distribution of species (e.g. Hewitt, 1999). It is usually considered that the Quaternary glaciations have influenced the present genetic structure of many species of terrestrial and freshwater habitats worldwide (Hewitt, 2004). During glacial periods numerous species in the Northern hemisphere were restricted to warmer Southern refugia, where populations may have been smaller and under different selection conditions, which would cause populations to diverge genetically (Hewitt, 1996, 1999). Re-colonization after the glacial period may have started from several refugia (Rundgren, 2007), which may have led to genetically differentiated populations in the re-colonized areas (Hewitt, 1996).

In addition, ongoing evolutionary processes (gene flow, genetic drift, selection) may be affected by more recent events such as environmental stressors (e.g. land-use, persistent soil contamination). The effects of environmental stressors on population genetic structure depend on the way evolutionary processes are affected. For instance genetic differentiation between stressed and non-stressed populations may occur due to selection of a particular character and/or due to an enhanced genetic drift when the environmental stressor leads to a decrease of the population size (Van Straalen and Timmermans, 2002). However, differentiation may be prevented

if gene flow among populations is significant (Van Straalen and Timmermans, 2002).

We surveyed the literature on population genetic structure of three groups of soil invertebrates: collembolans, earthworms and isopods, to evaluate their population genetic structure. The limited locomotion abilities of these organisms, which are associated with their soil-born life style, suggest the existence of highly structured populations. However, dispersal by passive mechanisms, such as wind and water, has been implicated in long-distance movement of these soil organisms and therefore gene flow may be sufficient to prevent genetic differentiation. An overview of the analysed literature is presented in Table 1. The bibliographic survey was performed on web of knowledge database considering the keywords: dispersal, genetic structure, collembolans, earthworms and isopods. Only studies considering genetic differentiation of field populations were considered.

## 2. Soil invertebrates

Soil-living collembolans, earthworms and isopods are important in organic matter decomposition processes, nutrient transformation and energy flow in terrestrial ecosystems (e.g. Drobne, 1997; Lee, 1985; Rusek, 1998). These animals are considered to have limited active dispersal capacities and therefore to be rather sedentary. Dispersal capacity is a life-history trait that is of ecological importance (Clobert et al., 2001; Mathieu et al., 2010) and directly affects the level of gene flow between populations.

Collembolans are generally considered to be unable to disperse over long distances due to the lack of wings and their small body size. Furthermore, many species are dependent on the edaphic environment, where they find the necessary moisture to avoid dehydration (Fanciulli et al., 2009). Sjögren (1997) studied several collembolan species (e.g. *Isotoma notabilis* Schäffer, *Isotomiella minor* Schäffer, *Folsomia quadrioculata* Tullberg and *Onychiurus armatus* Tullberg) in microcosm experiments, and reported an average dispersal rate of 1.4 cm per week. However, the dispersal capacity varies significantly among species (Hertzberg, 1997) with relatively large epigeic collembolans being more efficient dispersers than edaphic species (Ojala and Huhta, 2001). For instance, the epigeic collembolan *Orchesella cincta* (L.) has well-developed legs and antennae, which suggests capacity for mobility (Van der Wurff et al., 2003). Dispersal also depends on the availability of food, population density, and soil type (Bengtsson et al., 1994). However, predictions on dispersal based on anatomy may be misleading, as reported by Auclerc et al. (2009), whose results indicated the lack of a link between anatomical features and dispersal ability classes for half of the collembolan species they studied. This may be caused by the existence of passive dispersal mechanisms, such as wind, phoresy or egg transport.

In a mesocosm experiment Mathieu et al. (2010) showed that earthworms are capable of active dispersal to escape unsuitable environmental conditions, whether these are soil properties, litter content or population density. However, they are considered to have limited dispersal capacities of only a few meters per year; 1.5–14 m per year was estimated in several studies for five earthworm species (*Aporrectodea caliginosa* Savigny, *A. longa* Ude, *Lumbricus rubellus* Hoffm, *L. terrestris* L., and *Allolobophora chlorotica* Savigny) reviewed by Eijsackers (2011). Earthworms actively crawling over the soil surface will disperse considerably faster than species living in permanent burrows (Zorn et al., 2005). However, also anecic species actively disperse over the soil surface when they leave their burrows at night (Eijsackers, 2011 and references therein).

Isopods are assumed to travel over longer distances, as for example *Hemilepistus reaumuri* (Audouin) individuals that were found

**Table 1**  
Genetic structure of soil invertebrate species considered in this literature survey.

Species	Location	Genetic differentiation	Causes	References
Collembolans				
<i>Orchesella cincta</i>	Europe	High	Historical events; limited dispersal	Timmermans et al., 2005
	Netherlands	Low	Dispersal	Van der Wurff et al., 2003
	NW Europe	Low	Dispersal	Timmermans, 2005
	NW Europe	Low	Dispersal	Van der Wurff et al., 2005
<i>Tetradontophora bielensis</i>	Central/SW Europe	High	Historical events	Fanciulli et al., 1991
<i>Gressittacantha terranova</i>	Antarctica	High	Limited dispersal	Fanciulli et al., 2001
<i>Folsomia candida</i>	Aquifer	High	Limited dispersal	Sullivan et al., 2009
<i>Allacma</i> spp.	Italy	High	Historical events	Fanciulli et al., 2009
<i>Tomocerus</i> spp.	Italy	High	Historical events	Fanciulli et al., 2000
<i>Lepidocyrtus</i> spp.	NW Mediterranean	High	Historical events, limited dispersal	Cicconardi et al., 2010
<i>Desoria klovstadi</i>	Antarctica	High	Historical events, limited dispersal	Stevens et al., 2006
<i>Gomphiocephalus hodgsoni</i>	Antarctica	High	Historical events, limited dispersal	Stevens and Hogg, 2003
<i>Sminthurus viridis</i>	Australia	High	Limited dispersal	Roberts and Weeks, 2011
Earthworms				
<i>Lumbricus terrestris</i>	Germany	Low	Dispersal	Kautenburger, 2006
<i>Dendrobaena octaedra</i>	Canada	High	Multiple introduction events	Cameron et al., 2008
	Greenland/Canada/Europe	High	Historical events	Hansen et al., 2006
<i>Lumbricus rubellus</i>	Faroe Islands	High	Land-use	Enckell et al., 1986
<i>Aporrectodea rosea</i>	Finland	Low	Dispersal	Terhivuo and Saura, 1993
Isopods				
<i>Porcellio scaber</i>	Central Europe	Low	Historical events; dispersal	Wang and Schreiber, 1999a
<i>Oniscus asellus</i>	Central Europe	Low	Historical events; dispersal	Wang and Schreiber, 1999b

to disperse over a distance of 62–92 m per day (Warburg et al., 1984). For *Armadillidium vulgare* (Latr.) a smaller travel distance, of 1–13 m per day, was recorded (Paris, 1963). However, like collembolans, isopods are also strongly dependent on edaphic conditions and known to select microhabitats according to their moisture preference (Warburg et al., 1984). They furthermore have an inherent tendency to aggregate (Warburg, 1968), which may limit dispersal.

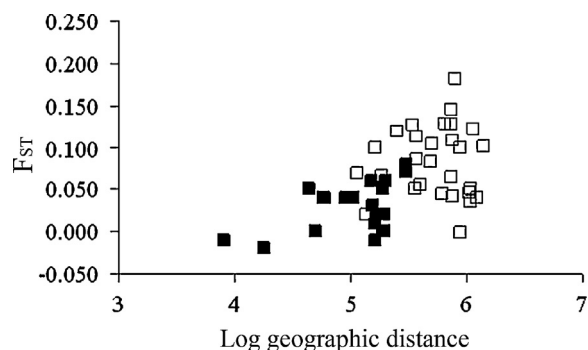
### 3. Population genetic structure of soil invertebrates

#### 3.1. Collembolans

Several studies on the population genetic structure of the collembolan *O. cincta* have been conducted at various geographical scales. Timmermans et al. (2005) sampled populations across a large part of its European distribution, extending from France to Poland and from Italy to Sweden. The results revealed the existence of three population clusters: NW Europe, Central Europe and Italy. The significant division between NW and Central Europe populations, in the absence of a clear geographic barrier was suggested to be due to re-colonization by individuals from different refugial areas during interglacial periods. Moreover, they suggested that the Alps form a barrier that prevents gene flow between Italian and the other European populations analysed. The existence of the Alpine barrier, causing isolation of Italian populations has been observed in other studies, for example with mammals and arthropods (e.g. Hewitt, 1999; Taberlet et al., 1998). A relatively high divergence between populations from Italy and Central Europe and a low differentiation among Central European populations was also found in the collembolan *Tetradontophora bielensis* (Waga) (Fanciulli et al., 1991). Gene flow among populations is also inhibited by other geological barriers. Genetic analysis of *Gressittacantha terranova* Wise from Antarctica revealed three genetically distinct groups with limited gene flow between them. Dispersal between populations is presumed to be hampered by glaciers that constitute efficient barriers (Fanciulli et al., 2001). Also, *Folsomia candida* Willem populations inhabiting a shallow lake-plain aquifer (2.5–5.7 m below surface) were found to be highly structured within an area of about 0.65 km<sup>2</sup> (Sullivan et al., 2009). The genetic differentiation was considered to be caused not only by the distance among populations (an isolation-by-distance pattern was observed) but also due

to the existence of barriers (possibly related with the geological characteristics of the aquifer) to gene flow. However, it has to be mentioned that the authors could not rule out local adaptation to have partially caused the observed pattern.

The significant population structure found among *O. cincta* European populations (previously mentioned) indicates limited gene flow among populations at a large geographical scale. However, when analysing *O. cincta* populations from a smaller geographic area (NW Europe) low population genetic differentiation and high levels of gene flow were observed. The existence of high gene flow was first revealed by Van der Wurff et al. (2003) who found low genetic differentiation between populations of two Dutch forests separated by 10 km. When considering populations sampled across the Netherlands (within a distance of 200–300 km), Van der Wurff et al. (2005) found low genetic differentiation and a weak isolation-by-distance pattern. A stronger isolation-by-distance pattern for NW European populations was revealed by Timmermans (2005) who showed that *O. cincta* populations over a distance up to 60 km were genetically undifferentiated, suggesting the existence of high levels of gene flow over such distances (Fig. 2). These results can be



**Fig. 2.** Relationship between genetic and geographic distance in the soil-living springtail *Orchesella cincta*. Geographic distance is measured in meters. Genetic distance is expressed as  $F_{ST}$  (Fixation index), estimated from six polymorphic microsatellite loci for pairwise comparisons between different populations from North-Western Europe. All populations were sampled from unpolluted forest soils. Open rectangles: data from Timmermans (2005); closed rectangles: data from Van der Wurff et al. (2005).

explained by the moderately high dispersal capacity of *O. cincta*, since species with such a dispersal capacity may be genetically homogeneous at small distances but differentiated over longer ones (Peterson and Denno, 1998). *O. cincta*'s tendency to climb trees has been suggested to facilitate wind driven dispersal over long distance up to 20 km (Freeman, 1952; Van der Wurff et al., 2003).

Contrastingly, within Italy some species, e.g. *Allacma fusca* (L.) and *A. gallica* (Carl), showed a high level of genetic differentiation (Fanciulli et al., 2009). Gene flow estimates indicated that the effective number of individuals that were exchanged between populations were insufficient to overcome effects of genetic drift. The authors also suggested that high levels of genetic differentiation could have been due to bottleneck events during Plio-Pleistocene geological rearrangements that took place in the peri-Tyrrhenian area. Yet, an isolation-by-distance pattern was observed for both species, demonstrating the presence of some degree of gene flow among geographically close populations, most probably originating from passive dispersal of individuals by either wind and/or animals transport. Fanciulli et al. (2000) reported strong population differentiation in four Collembola species (*Tomocerus vulgaris* (Tullberg), *T. minor* (Lubbock), *Pogonognathellus flavescens* (Tullberg), and *P. longicornis* (Müller)) caused by Plio-Pleistocene geological rearrangements coupled with genetic drift and limited gene flow. Historical events, in the late Miocene, were also considered responsible for the genetic differentiation found within the genus *Lepidocyrtus* Bourlet from the North-western Mediterranean basin (Cicconardi et al., 2010). The authors found a geographic structure with highly differentiated genetic lineages and no evidences of gene flow, even across distances of only tens of kilometres. Also, a phylogeographic analysis of *Desoria klovtadi* Carpenter revealed the effects of long-term historical fragmentation, due to Pleistocene and Holocene glacial cycles, and limited gene flow among populations (Stevens et al., 2007). Genetic differentiation were also found in *Gomphiocephalus hodgsoni* Carpenter populations from Victoria Land, Antarctica, probably caused by the Pleistocene glaciations along with limited dispersal. However, human- and/or birds-mediated dispersal as been presented as a possible explanation for the mixing of identical haplotypes (Stevens and Hogg, 2003).

Roberts and Weeks (2011) studied another collembolan species, *Sminthurus viridis* (L.), from several regions in Australia, where it was introduced from Europe in the late 1800s. Results revealed significant population genetic structure, suggesting limited gene flow. Yet, the fact that distant populations were less differentiated than populations close to each other weakened the isolation-by-distance relationship (see Fig. 1). The observed pattern was explained by the possible existence of long-distance dispersal mediated by human activities (such as the transportation of animal fodder, seeds and soil).

Considering the studies mentioned above, geological barriers and historical events are the main factors responsible for the genetic structure found among collembolans populations. The genetic homogeneity found in some cases may be explained by wind and/or animals-mediated gene flow. In addition, anthropogenic transport of soil or other materials can influence population genetic structure of collembolans.

### 3.2. Earthworms

The population structure of several earthworm species has been analysed. Kautenburger (2006) studied *Lumbricus terrestris* L. sampled in different locations in Western Germany. A similar genetic structure was observed among neighbouring locations up to about 20 km apart. Populations located at more than 70 km apart were found to be genetically differentiated. However, gene flow among adjacent populations did not lead to a trend of increasing genetic

differentiation with geographic distance on a larger scale. The absence of an isolation-by-distance pattern suggests a complicated pattern of gene flow between earthworm populations. Cameron et al. (2008) studied populations of *Dendrobaena octaedra* Savigny from Alberta (Canada). The introduction of this species in the boreal forests of Alberta was suggested to be mediated by anthropogenic activities (e.g. bait abandonment), with the recurrent nature of these introductions resulting in significant population differentiation. No relationship between genetic and geographic distances was found, which strengthens this view and indeed suggests that such "jump dispersal" is of greater importance than diffusive spread (along road networks) and active dispersal. This is consistent with the idea that earthworms have a limited capacity to autonomously disperse (Marinissen and Van den Bosch, 1992; Sakai et al., 2001) and so their dissemination will often be due to anthropogenic or animal-mediated transport, causing erratic genetic distribution patterns. A strong genetic differentiation among Greenlandic and Canadian/European populations of *D. octaedra* was found by Hansen et al. (2006), which suggests that dispersal between Greenland and the continental locations has been more restricted than dispersal among continental areas. The authors suggested that populations from Greenland have persisted for a long period, surviving glacial periods in local ice-free refugia. Two hypotheses for post-glacial colonization of Northern Europe are usually considered: re-colonization from local ice-free refugia (refugium hypothesis) and re-colonization from southern regions (tabula rasa hypothesis); more information may be found in Rundgren (2007). The existence of clones shared among different localities in Greenland was suggested to be the result of (human-mediated) passive transportation.

Enckell et al. (1986) studied *L. rubellus* at the Faroe Islands. The authors found a weak relationship between genetic and geographic distance and showed that geographical barriers had only slight or no influence on genetic variation between different populations. The genetic differences found between the populations from the infields and the outfields appear to be caused by selective effects of land-use (e.g. eutrophication of the infields). It is known that land-use practices affect earthworm's species diversity, however, further studies should be performed to assess if genetic diversity is also affected as in the case-study mentioned above. Terhivuo and Saura (1993) revealed a high clonal diversity of *Aporrectodea rosea* (Savigny) in southern Finland, attributed to dispersal through agricultural activities. Human activities are also the major dispersal strategy for *Octolasion cyaneum* Savigny in North Europe (Terhivuo and Saura, 1997). Other forms of dispersal, as the one mediated by flowing water, occurred in species such as *Eiseniella tetraedra* Savigny, *D. octaedra* and *Octolasion tyrtaeum* Savigny (Terhivuo and Saura, 2006). Taken together, these studies reveal that the population genetic structure of earthworms is strongly influenced by human activities.

### 3.3. Isopods

Regarding isopods, Wang and Schreiber (1999a, 1999b) analysed the genetic structure of central European populations of the species *Porcellio scaber* Latr. and *Oniscus asellus* L. Low genetic differentiation among nearby locations (10 km) was observed and isolation-by-distance was found on a larger geographic scale. The results of both studies were explained by the fact that the time elapsed since re-colonization of Central Europe after Pleistocene glacial periods from southern refugia was not enough to allow genetic differentiation to occur. Furthermore, the high abundance and therefore presumed large population sizes of these isopod species could buffer the effects of genetic drift. The authors finally suggested that the observed genetic homogeneity among populations could be due to passive dispersal, i.e. mediated by wind,



flowing water or human activities (e.g. translocation of compost, plants, and agricultural products). *P. scaber* was passively introduced through human activities (transportation of building materials) on the sub-Antarctic Marion Island (Slabber and Chown, 2002). Like for the collembolan *O. cincta*, vertical migration towards tree tops might facilitate dispersal by wind in some isopod species (Brereton, 1957; Den Boer, 1961).

#### 4. Conclusions

Despite the limited active dispersal capacities of soil invertebrates such as collembolans, earthworms and isopods, populations of several species were found to be genetically undifferentiated over considerable distances. Passive dispersal, either mediated by wind, water flow or animals has been implicated in the maintenance of genetic homogeneity in these cases. Clear evidence of genetic differentiation increasing with distance is seen mainly at a larger scale (e.g. >60 km in the collembolan *O. cincta*). Population structure of soil invertebrates reflects historical events, such as re-colonization after glaciations. Despite the few studies available, with relatively diverse data and based mostly on allozyme markers, this review intended to summarize the actual knowledge on population genetic differentiation of some fauna groups. More information on the genetic variation of soil invertebrates is expected to come from genome-wide polymorphism studies. Such population-genomics approaches may further improve molecular-based estimates of population genetic parameters, such as effective population size, population structure and dispersal rates (Luikart et al., 2003).

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