Applied Soil Ecology xxx (xxxx) xxx–xxx

Contents lists available at ScienceDirect

Applied Soil Ecology

journal homepage: www.elsevier.com/locate/apsoil

Short communication

Methods for studying earthworm dispersal

Jérôme Mathieu[a,*], Gaël Caro[b], Lise Dupont[c]

[a] Sorbonne Universités, UPMC Univ Paris 06, UPEC, Paris 7, CNRS, INRA, IRD, Institut d'Ecologie et des Sciences de l'Environnement de Paris, 75005, Paris, France
[b] UMR 1121, Université de Lorraine – INRA, Laboratoire Agronomie et Environnement, 2 Avenue Forêt de la Haye, 54518 Vandoeuvre, France
[c] Université Paris Est Créteil (UPEC), UPMC Univ Paris 06, Paris 7, CNRS, INRA, IRD, Institut d'écologie et des sciences de l'environnement de Paris, 94010 Créteil Cedex, France

ARTICLE INFO

Keywords:
Movements
Landscape structure
Connectivity
Behavior
Capture mark recapture methods

ABSTRACT

Dispersal is a key driver of species composition and functional traits in earthworm communities. However, it has been largely overlooked in ecological literature on earthworms because it is particularly difficult to study. In this publication, we review recent developments that have been made in this field of research. We present methods to assess dispersal distance, such as Capture-Mark-Recapture and molecular tools, and methods using dispersal corridors or X-ray imagery aiming at identifying the mechanisms triggering dispersal in earthworms communities.

1. Introduction

Dispersal plays a major role in shaping biodiversity, evolution, and ecosystem functioning. It connects localities together through fluxes of individuals and alleles. The direct consequence is that species abundance and genetic composition in different places of a landscape are not independent. In other words, local population abundance, genetic structure and community structure not only depend on local factors and processes such as habitat features, demography, genetic drift or species sorting and competition, but are also dependent on the properties of neighboring populations and communities (Leibold et al., 2004). In this perspective, we need to study local community and genetic structure at both local and regional scales in order to understand the structure of local populations or communities, as well as their functional role.

The magnitude of the dependence between local and regional scales directly results from dispersal rate. Theoretically, when dispersal is very high, local sites are well interconnected and tend to behave like a unique population or community (Economo and Keitt, 2008; Mouquet and Loreau, 2003). Local interactions are then a major driver of species composition and a low genetic differentiation among populations is expected. When dispersal is very low, local sites are isolated and behave like islands. Local populations and communities are well differentiated and severe genetic drift occurs. Extinction risk is then high for small populations. In nature, dispersal is generally between these two extremes, and complex behaviors such as source – sink dynamics may occur. In such case, certain sites can act as sources of dispersers (source), while others behave like sinks. Such dynamics can prevent extinction or speciation in certain sites. Local populations connected by dispersal are called "metapopulation" (Hanski and Gilpin, 1997), local communities connected by dispersal are called "metacommunity" (Leibold et al., 2004). In both cases, we need to understand the drivers and the magnitude of dispersal in order to understand the behavior and the properties of the system, either at local and regional scales.

Dispersal is usually defined as the movement of individuals away from their natal habitat, or from their usual home range, to a new habitat (Clobert et al., 2012). It is usually decomposed in three successive steps. First step is departure from the usual home range. Second is the transfer between the departure site and the arrival site. Third is the establishment in a new habitat (Fig. 1).

All these steps can originate from two very distinct processes: it can come from individuals' own willing, a process called "active dispersal", or from movements driven by an external force such as wind, water runoff, displacement by another animal, or by human activities (Matthysen, 2012). Dispersal direction is generally controlled in active dispersal but not in passive dispersal.

Studying dispersal is challenging for all organisms (Nathan, 2001), because it is hard to track individuals. This is particularly true for earthworms, because they are subterranean and cannot be seen from surface. Several approaches have been developed to address these difficulties, and can be classified in two groups. The first ones focus on dispersal patterns. They intend to measure typical dispersal distances of organisms during life span, or during a precise period of time. This approach aims at producing a histogram of distances travelled over a period of time, the so called "dispersal kernel" (Nathan et al., 2012). It is thus centered on the spatio-temporal aspects of the dispersal. The second group of methods focuses on the factors that drive dispersal,

* Corresponding author.
E-mail address: jerome.mathieu@upmc.fr (J. Mathieu).

http://dx.doi.org/10.1016/j.apsoil.2017.09.006
Received 16 December 2016; Received in revised form 30 July 2017; Accepted 2 September 2017

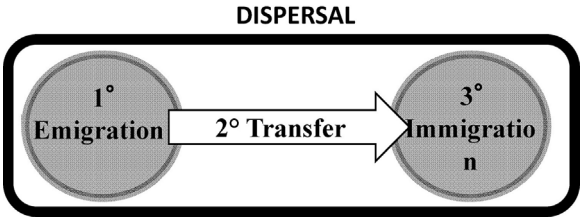

Fig. 1. Dispersal is usually decomposed in three steps: Emigration from the source, transfer, and immigration to a new site.

such as habitat quality or conspecific density. The products of this approach are dispersal rules, like positive density dependent dispersal. This approach is often framed in game theory and evolutionary ecology. It aims at predicting dispersal behavior and understanding the reasons why different dispersal behaviors evolved.

In this work, we present techniques that are currently available to study earthworms' dispersal from these two angles: 1) dispersal distances and 2) the factors that drive dispersal.

2. Methods for studying earthworm dispersal distance

One of the most basic question regarding dispersal of organisms is to determine how far they can move. In order to address this point, we need to estimate the distribution of the distances travelled for a given period of time. For this, two kinds of movements are often defined: the usual and most frequent movements, related to foraging, and the rare long distances movements (Nathan et al., 2008). In this framework, true dispersal usually refers to the rare and long distances dispersal events (LDD), located in the tail of the dispersal distribution (Nathan et al., 2012). These rare events play a critical role in colonization processes and invasion processes (Trakhtenbrot et al., 2005).

The estimation of traveling distances is challenging for earthworms, but can be done in two broad ways: by tagging and by studying the genetic profiles of individuals or populations.

2.1. Tags

Methods based on tags usually share the same principle: a group of individuals is captured, marked with a tag, then released at a known location in the field or in an experimental device. After a period of time, the marked individuals are searched at proximity from the release point. The distribution of the recapture distances from the release point (Fig. 3A) gives the "dispersal kernel" of the individuals over the respective period of time. These methods are generally referred to as Capture Mark Recapture (CMR) methods (Seber, 1982). They are better suited for short distances estimation than for LDD. In theory, individuals can be released and recaptured several times, but this is difficult to achieve in the field on earthworms. Variations in CMR methods include the type of tags, the capacity to use tags specific to individuals, and the number of recapture events. In earthworms, several types of tags have been used so far. Early attempts used food colorants such as E102 + E132 (green) or E124 (red) and red biological stains such as Safranin and Phloxine (Mazeaud, 1979). More recently, $^{15}NH4+$ and U-^{13}C glucose (Dyckmans et al., 2005), Rubidium (Ben Hamou et al., 2007), or ^{60}Co (Capowiez et al., 2001) have been used with success. However, all these methods are difficult to apply because they require a significant equipment or lab work to detect the tags, because they are not visible with naked eyes. We now present in detail two recent methods that circumvent these caveats.

2.1.1. Visual tags for earthworm: VIE

Visible Implant Elastomers (VIE, Figs. 2 A & B and 3 A) are colored tags that are injected below the skin (Butt and Lowe, 2007; Gonzalez et al., 2006). They are injected in a liquid state but soon become solid through a polymerization process. They are available from Northwest Marine Technology, Inc. (http://www.nmt.us/) and are relatively affordable.

This kind of tags has been used with success on a variety of organisms such as fish, frogs, turtles and seeds, in order to assess population size or dispersal distance. They are visible through the skin of the animals, particularly with a UV light. The tags are well supported by earthworms (Butt et al., 2009). They can stay up to 27 months in their body, which is much longer than the previously mentioned tags (Butt et al., 2009).

The main drawback of this method is the impossibility of monitoring individuals in a continuous manner. It is not possible to track individuals between two capture events. Marking and recapturing require a lot of time, and tags are hardly specific to individuals, even though combining tags of different colors is possible for large individuals (> 1.5 g, Fig. 2B). This method requires releasing a high number of marked animals for statistical reasons, which can trigger density dependence dispersal (McCrea and Morgan, 2014). Indeed, in many species, high level of conspecific density leads to active dispersal (Caro et al., 2013; Mathieu et al., 2010). Finally, statistical methods for capture recapture data are complex (Amstrup et al., 2005; Lee and Chao, 1994). Despite these difficulties, this approach is very useful to get an estimation of the dispersal kernel of individuals.

2.1.2. Electronic tags: RFID tags

A new promising technique is the use of miniaturized RFID tags (Radio Frequency IDentification). These tags (Fig. 4) offer the possibility to mark each individual specifically, with a unique barcode ID. A scanner (Fig. 4B) retrieves the ID of an individual when the tag is close enough from the receptor, typically less than 0.5 cm.

Detecting individuals in a continuous fashion can be achieved by installing antennas at the surface of the ground, which detect any individual with a tag that comes close to the antenna. This offers the possibility to track individuals continuously and at different sites.

This method suffers from several limitations that still impede its use on a regular base. First, RIFD tags are more harmful than VIE tags. They are bigger (1.4×8 mm) and are frequently ejected out of the body by earthworms. During preliminary tests, only larger individuals, typically > 1 g, supported them. Second, detection can only be done at very short distance from the antenna (< 0.5 cm), and cannot be done through the soil. Even if the antenna can be buried, it is much more efficient to detect individuals on the surface. Thus, this technique is better suited for large epigeic and anecic species, which crawl on surface, but not for endogeic ones. Third, the tags are completely invisible once injected, which makes it difficult to find their location in the body during manual scanning, or to determine if an individual is tagged or not. A VIE can be injected in addition, close to the RIFD tag, however this increases the risk of mortality. At the moment, miniaturized RFID can only be detected by the scanners provided by the RFID manufacturers, which are expensive and have a limited efficiency. However, in the future it should be possible to build its own system of scanners or antenna and data logger.

2.2. Molecular approach

Recent progresses in molecular biology offer new opportunities for the estimation of dispersal distance of earthworms from genetic data (Dupont, 2009; Torres-Leguizamon et al., 2012; Zeller et al., 2012). As dispersal leads to gene flow, genetic information can be used to infer dispersal patterns. They can be assessed in two ways: first by comparing observed populations' genetic structure to theoretical ones under no dispersal, and second by statistical assignment methods that allow identifying the parents or the population of origin of individuals, based on their genetic profile (Broquet and Petit, 2009). In addition, the effect of landscape structure on dispersal patterns can be assessed with the tools developed within the framework of landscape genetics (Manel