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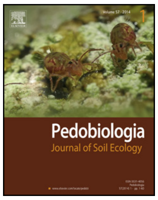

# Density-dependent responses in some common lumbricid species

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ABSTRACT

It is generally accepted that populations of most species experience some level of density dependence; however, this has rarely been shown for soil-dwelling invertebrate species, in particular for earthworms. Experimental data, mostly obtained at high laboratory densities, suggest intense intraspecific competition for resources and/or living space and density-dependent dynamics in earthworm populations, irrespective of their ecological group affiliation. In the present study performed in large field microcosms, I investigated whether density-dependent responses occur within the earthworm density gradients more realistic for the natural sites. Five lumbricid species from epigeic (*Dendrobaena octaedra*, *Lumbricus rubellus*), endogeic (*Allolobophora chlorotica*, *Aporrectodea caliginosa*) and anecic (*Lumbricus terrestris*) ecological groups were tested. Soil systems populated with earthworm monocultures in large (20-L) microcosms were exposed in a beech-oak forest for 4.5 months; each species was represented by two (*L. terrestris*) or three treatments forming gradients of increasing density. In two endogeic species, manifold and generally similar density-dependent responses (a retardation of growth, maturation and reproduction rates, but higher mortality rates with density increase) were revealed, likely explained by spatial competition rather than by direct food competition. In each of epigeic species density-dependent responses were less variable and more species-specific. In contrast to endogeics, direct food competition was presumably a more important cause of density-dependence. In *L. terrestris* no significant density-dependent responses in adult earthworms were revealed; however, they need to be further investigated in relation to the age and territorial behaviour of individual earthworms. Importantly, in any earthworm species the density variations in the reproducing generation had significant consequences for the advancing generation, affecting either the numbers or/and the size (individual weight) of the cocoons produced. It is suggested that an underestimation of density-dependent processes may cause inaccurate estimates of the activities of local lumbricid populations.

## 1. Introduction

It is generally accepted that both density-independent and density-dependent processes operate in natural populations and that populations of most species experience some level of density dependence (Brook and Bradshaw, 2006; Hixon and Johnson, 2009). Having performed a multi-model inference analysis of a dataset of time-series observations for 1198 species, Brook and Bradshaw (2006) indicated a support of 74.7% for the density dependence, and even a higher one (78%) concerning invertebrates (639 species). This dataset, however, did not include soil fauna (except for three soil surface-active carabid species); overall it may be noted that information on population dynamics of soil-dwelling invertebrate species, in particular of earthworms, is very scarce.

After Hixon and Johnson (2009), competition (for food resources, living space, etc.) is one of the main causes of density dependence. Field densities of earthworm populations are extremely variable in space and time in species of any ecological group, ranging from single specimens to thousands of individuals m$^{-2}$ (Petersen and Luxton, 1982; Lee, 1985; Uvarov, 2009). Strong intrabiotopic density variations also occur across the seasons of the year and due to aggregative distribution of many lumbricid species (Phillipson et al., 1976; Holter, 1983; Boag et al., 1994). This suggests an intense intraspecific competition in earthworm populations, at least during some periods and within the patches of higher densities, and potentially a density-dependent population dynamics. However, intraspecific responses of earthworms to population density variations are still insufficiently investigated. It may be

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suggested that an underestimation of density-dependent processes may cause inaccurate estimates of the local activities of lumbricid populations and, considering the significance of earthworms as engineering organisms (Eisenhauer et al., 2007; Briones, 2014; Filser et al., 2016), of the functioning of detrital food webs and organic matter turnover in the soil.

The majority of the experimental investigations of intraspecific relations in earthworms, as reviewed by Uvarov (2009), support density-dependent regulation of species populations, irrespective of their ecological group affiliation. Usually negative density-dependent population responses have been revealed, i.e. at higher density levels the growth, maturation and reproduction rates are retarded, whereas the mortality rates are increased. However, these results have almost exclusively been obtained in laboratory experiments mostly performed in small microcosms populated by very dense earthworm groups.

The purpose of the present study was to investigate whether density-dependent responses are significant for earthworm species within the density gradients realistic in the natural sites. Five common lumbricid species belonging to the main (epigeic, endogeic, anecic) ecological groups were chosen for a field experiment conducted in a mid-European beech-oak forest. The duration of the experiment (ca. 4.5 months in the summer/autumn season) was sufficient to estimate the response trends of the essential population parameters (changes of population biomass, mortality and reproduction rates, mean weights of earthworm individuals and cocoons). The hypotheses assumed (1) the presence of density-dependent responses in all of the species studied, and (2) a stronger expression of density dependence in the litter-feeding species compared to endogeic ones, due to more restricted amounts of organic matter resources (hence, a potentially more intense trophic competition) in the litter than in the soil.

## 2. Materials and methods

### 2.1. Study site and weather conditions

Litter and soil were collected in a beech-oak forest located in the Mazury Landscape Park (northern part of Piska Forest, NE Poland, 53°43 'N and 21°36 'E), in the beginning of June 2006. Undergrowth were lime, hazel and maple; soil plant cover was nearly absent. Overwintered litter 2–4 cm deep was weakly stratified (L + F/H) and mainly consisted of oak, beech and lime leaves markedly processed by soil biota. A weakly structured sandy soil was haplic arenosol (FAO/UNESCO classification); A horizon was 15 cm deep, pH($H_2O$) was 5.5. The carbon content of the litter and soil (A horizon) was 37.3 and 2.7%, while the nitrogen content 1.6 and 0.17%, respectively. The materials (FH-litter and soil from A horizon) were transferred 5 km N to the Mikolajki Hydrobiological Station (then belonging to the Centre for Ecological Research, Polish Academy of Sciences) where the experiment was conducted in a beech-oak grove.

The summer–autumn season of 2006 was by 1.5–2° warmer (air temperature) and more rainy than the average weather conditions during the decade of 1996–2005 (as compiled using the site www.weatheronline.co.nz for Mikolajki, Poland). The temperature regime in the microcosms was monitored at the litter/soil interface at 2 h intervals by means of data loggers. Monthly temperatures were 17.9, 16.0, 14.2, 10.5 and 5.2 °C in July–November, respectively. The moisture conditions were ca. 65% of microcosm water holding capacity at the start and were kept favourable by regular watering (at 10–14 d intervals in the summer, rarer in the autumn). The amount of water added (totally 461 mm in July–November) corresponded to the precipitation of the rainy summer/autumn of 2006 (417 mm); excessive water was easily drained through the gauze bottom of the microcosms.

### 2.2. Microcosms

Microcosms were plastic cylinders 60 cm high and 20 cm in inner diameter, with an air/water-tight lid; the lid had a 2 cm round hole for air exchange. Both the lid hole and the bottom of the cylinders were sealed with gauze to prevent earthworms from escape. In the microcosms, which were half-dug into the soil, soil columns were established resembling the soil structure in the field: 9.5 L of soil (30 cm deep) were covered with 100 g of overwintered litter. This corresponded to ca. 2.1 kg dwt $m^{-2}$ and was at the higher limits of the range of litter supply reported for Eurasian broadleaved forests (1–2 kg dwt $m^{-2}$, after Bazilevich, 1993). The levels of the soil/litter interface inside and outside the microcosms corresponded to one another. The soil had been sieved (4 mm) for homogenization and the removal of roots, earthworms and macrofauna. The FH litter material had been sorted to remove earthworms and macrofauna predators, and mixed. To further equalize the starting conditions, and compensate for microbiota losses during the litter preparation, 50 mL of water suspension prepared from the untreated litter were added into each microcosm.

### 2.3. Treatments and sampling

The prepared microcosms were kept for ca. 3 weeks in the field for soil system establishment, and then populated by earthworms. Five common European lumbricid species were used in the experiment: *Dendrobaena octaedra* Savigny (1826); *Lumbricus rubellus* Hoffmeister, 1843; *L. terrestris* L., 1758; *Allolobophora chlorotica* (Savigny, 1826); *Aporrectodea caliginosa* (Savigny, 1826). The species represented three main earthworm ecological groups: epigeic (*D. octaedra* and *L. rubellus*), anecic (*L. terrestris*) and endogeic (*Al. chlorotica* and *A. caliginosa*). Earthworms were collected during June – early July in Piska and Kampinos Forests, and kept in soil/litter containers at 4 °C until the beginning of the experiment. Specimens of *L. terrestris* were expelled from the soil by syringe-injecting of a 0.15% formalin solution into their burrows; earthworms of other species were collected by handsorting of the litter or soil.

At the start of the experiment, *Lumbricus* spp. and *D. octaedra* were represented by adult worms, *A. caliginosa* by large juveniles, and groups of *Al. chlorotica* contained 40% adults and 60% large juveniles. Before being placed into the microcosms, and during the terminal microcosm sampling (below), the living weight of earthworm individuals was determined after keeping for 24 h on wet filter paper to void their guts. The earthworms were introduced into the microcosms on 10.07.2006; the experiment was terminated (microcosms destructively sampled) after 130 d., on 16.11.2006.

In each earthworm species, a gradient of density increase (minimum – medium – maximum treatments) was established in the microcosms; the actual densities depended on species size. Thus, for the smaller species (*D. octaedra* and *Al. chlorotica*) the respective densities comprised 5–15–25 ind. $microcosm^{-1}$; for the medium-sized animals (*L. rubellus* and *A. caliginosa*) they were 3–9–15 ind. $microcosm^{-1}$. In the largest species (*L. terrestris*), only two density levels were tested: 2 and 3 ind. $microcosm^{-1}$. The earthworm densities in the microcosms generally corresponded to ranges lying between moderate/moderately high and high species densities in the natural sites (ca. 150–750 ind. $m^{-2}$ in *D. octaedra* and *Al. chlorotica*, 90–450 ind. $m^{-2}$ in *L. rubellus* and *A. caliginosa* and 60–90 ind. $m^{-2}$ in *L. terrestris*). Each treatment had 4