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Productivity affects the density–body mass relationship of soil fauna communities

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A B S T R A C T

The productivity of ecosystems and their disturbance regime affect the structure of animal communities. However, it is not clear which trophic levels benefit the most from higher productivity or are the most impacted by disturbance. The density–body mass (DBM) relationship has been shown to reflect changes in the structure of communities subjected to environmental modifications, so far, mainly in aquatic systems. We tested how different seawater inundation frequencies and cattle grazing, which both disturbed and impacted the productivity of a terrestrial system, a salt marsh, affected the size structure of soil fauna communities, expressed by their DBM relationship. We hypothesized that either: (1) all the trophic levels of soil fauna would benefit from higher productivity (i.e., amount of litter mass), reflected by a higher *Y*-intercept of the DBM relationship; (2) only smaller animals would benefit, reflected by a lower slope of the relationship; (3) or only larger animals would benefit, reflected by a higher slope of the relationship. We collected a large range of soil fauna from different elevation levels in grazed and ungrazed areas, thence subjected to different levels of productivity, represented by litter mass, with the most inundated and grazed area as the least productive one. Considering that pore size must be smaller in inundated and grazed areas, productivity seemed to be a greater factor influencing species distribution than soil structure. We found slopes lower than −0.75, showing that large animals dominated the community. However, a difference between the DBM relationships of the most and least frequently inundated ungrazed sites indicated that higher productivity benefited the smaller animals. Our findings show that high productivity does not equally affect the different trophic levels of this soil fauna community, suggesting inefficient transfers of energy from one trophic level to another, as smaller species benefitted more from higher productivity.

1. Introduction

The composition of plant and animal communities usually depends on ecosystem productivity (Waide et al., 1999; Evans et al., 2005; Gillman and Wright, 2006) as well as on the impacts disturbances have on those communities, the latter still being debated (Fox, 2013; Sheil and Burslem, 2013). The mechanisms underlying those effects of productivity and disturbance remain unclear to date (Gillman and Wright, 2006; Adler et al., 2011). As they differ depending on the trophic levels of the community (Wootton, 1998), a relevant indicator of the functioning of communities may be the size structure of communities, i.e. the distribution of the sizes of the plants or animals of a community (Giometto et al., 2013). Thus, in this study, we used the relationship linking soil fauna's density to their body mass in order to test how productivity and disturbance affect the structure of communities. As many of the studies on this topic have considered aquatic systems (Sheldon et al., 1972; Strayer, 1986; Marquet et al., 1990; Cyr et al., 1997a; Schmid et al., 2000; Thygesen et al., 2005) and few have focused on terrestrial ecosystems (Aava-Olsson, 2001; Reuman et al., 2009), this study gives some new insight in how soil fauna communities are structured as function of productivity and disturbance.

A common metric of the size structure of communities is the relationship between the animals' density and body mass (Peters and Wassenberg, 1983). It includes variations of one of the most

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relevant traits regarding the functioning of animal communities, the body mass of individual species (Lawton, 1990; Saint-Germain et al., 2007). The latter encompasses many of the species life-history traits (Peters, 1983; Peterson et al., 1998; Lewis et al., 2008), as it relates to ecological, physiological and behavioural aspects of animals (Damuth, 1987). A negative relationship between animal density (D) and body mass (M) has received empirical and theoretical support, with $D = a \cdot M^b$, where the exponent b is approximately −0.75 for taxa within a single trophic level (Brown et al., 2004; Damuth, 1981, 1987). When considering several trophic levels, b has been reported to be close to −1 (Peters and Wassenberg, 1983; Boudreau and Dickie, 1992; Schmid et al., 2000).

The more productive an ecosystem is the more organisms it can support (McGlynn et al., 2010), inducing an increase in species richness and/or abundance of its communities following the increase in productivity (i.e., the species – energy hypothesis (Wright et al., 1993)). Conversely, as a stress or a disturbance decreases the productivity of an ecosystem and modifies its habitat (Sousa, 1984), the abundance within each species may decrease and some species may even disappear because they cannot compete anymore for the scarce resources and/or survive in the harsher environmental conditions (i.e., competitive exclusion (Hardin, 1960)). The functioning of a community, and consequently its response to productivity and disturbance, is determined by species-specific life-history traits (McGill et al., 2006). Therefore, the relationship between the animals' density and body mass can reflect variations of the structure of communities due to environmental changes (Cyr et al., 1997a; Reuman et al., 2009), because of the changes in species richness and abundance (and hence, changes in body mass distribution) of the communities (Leaper and Raffaelli, 1999). However, despite the "energetic equivalence rule" (Nee et al., 1991) predicting that population energy use per unit area (the product of density and individual metabolic requirements) is approximately independent of body mass, it is yet unclear whether this rule is expected to be found across different levels of productivity (Loeuille and Loreau, 2006; Buckley et al., 2008). This could be due to the inefficient transfer of energy between trophic levels (Maxwell and Jennings, 2006; Reuman et al., 2008).

In this study, we tested how the combination of two factors, i.e., various seawater inundation frequencies and cattle grazing, both disturbing the studied system and creating several levels of productivity, affects the structure of soil fauna communities represented by the relationship between the animals' density and body mass. The latter may change according to one of three alternative hypotheses (Fig. 1). Hypothesis 1: based on the energy limitation hypothesis, which states that the total abundance of organisms within an ecosystem is limited by the available energy (Wright, 1983; Currie, 1991), we hypothesized that the total number of animals, irrespective of their body mass, would increase if productivity increases, thus not changing the slope of the relationship, but only increasing the Y-intercept. Hypothesis 2: if mostly small organisms benefit from a higher productivity because of the inefficient transfer of energy to higher trophic levels (Cotgreave, 1993; Marczak et al., 2007), then an increase in productivity would result in a lower (steeper) slope of the relationship (Cyr et al., 1997a). Hypothesis 3: if more resources are available to species of higher trophic levels, which are generally larger, than to species of lower trophic levels, then an increase in productivity would result in a higher slope of the relationship. For instance, it has been shown that more nutrients can benefit species of the lowest (e.g., plants) and highest trophic levels (predators) of a community without affecting the species of the intermediary trophic levels (herbivores or decomposers) (Abrams, 1993). Both cattle grazing and the presence of water have an effect on the soil structure: trampling reduces the size of the soil pores (Schon et al., 2011) and so does a high inundation frequency (Blom and Voesenek, 1996) and that may affect the size spectrum of the soil fauna community (Andresen et al., 1990). Consequently, soil fauna may not only be sensitive to productivity, but also to the structure of their habitat (Giller, 1996) and smaller animals may be favoured in grazed and frequently inundated areas.

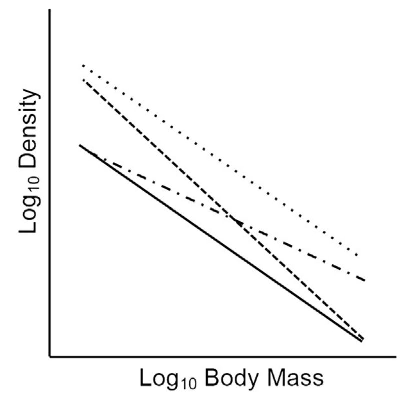

Fig. 1. Expected relationships between the density and the body mass of the soil fauna communities from sites with different productivity levels. Continuous line: low productivity site (i.e., with a high frequency of inundation); doted line: expected slope if the total abundance of all the animals increases with increasing productivity, irrespective of their body mass: only the Y-intercept would become higher (Hypothesis 1); short-dashed line: expected slope when mostly small organisms benefit from a higher productivity: slope would decrease and higher values would be found for the coefficient b of the DBM relationship (Hypothesis 2); long-dashed line: expected slope if more resources are available to species of the higher trophic levels, which are generally larger, than to species from lower trophic levels: slope would increase and lower values would be found for the coefficient b of the DBM relationship (Hypothesis 3).

Several methods exist to analyse the relationship between the animals' density and body mass of a community (White et al., 2007; Reuman et al., 2008). As we used several methods to sample the soil fauna, focussing on three distinct main groups (i.e., nematodes, Collembola and macrofauna), we opted for the density–body mass (DBM) relationship (Cyr et al., 1997b; Reuman et al., 2008): this relationship shows the representation of the density against body mass of the dominant species. To be able to better understand and interpret the results of the DBM relationship, we also measured the total density and biomass of soil fauna, as well as the average body mass per individual of each community along the productivity gradient.

To test our hypotheses, we conducted an experiment in the coastal grassland of a salt marsh showing a gradient of productivity caused by different frequencies of seawater inundation periods and by cattle grazing. We monitored the response of the soil fauna community, which is largely affected by litter mass (David et al., 1991; Scheu and Schaefer, 1998; Chen and Wise, 1999). Hence, differences in litter mass were used to represent different levels of productivity. The most frequently inundated areas (closest to the sea) and the grazed areas were expected to be the most disturbed ones, hence having the lowest litter mass and being the least productive compared to the rarely inundated and non-grazed ones (Bakker, 1985; Schrama et al., 2012). The objective of this study was to determine which part of soil fauna body size spectrum benefits the most from a higher productivity in order to better understand the energy distribution within a community.

2. Material and methods

Fieldwork was carried out on the salt marsh of the barrier island of Schiermonnikoog, the Netherlands (53°28′43″N, 6°14′06″E) in October and November 2011. We selected seven plots (2 × 2 m)