

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



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ABSTRACT

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.

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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

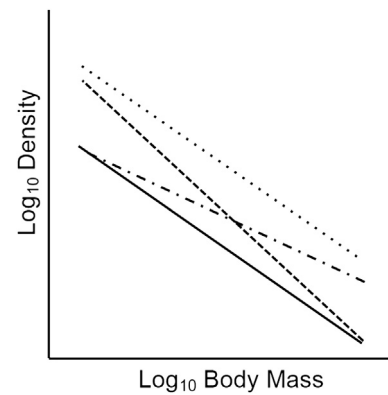


Fig. 1. Expected relationships between the density and the body mass of the soil fauna communities from sites with different productivity levels. Continuous line: low productivity site (i.e., with a high frequency of inundation); dotted line: expected slope if the total abundance of all the animals increases 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).

high inundation frequency (Blom and Voeselek, 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.

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)

based on the differences of basal elevation, which determines the inundation frequency by seawater: daily, weekly, monthly and annual inundation represented low, lower middle, upper middle and high salt marsh zones respectively (Hacker and Bertness, 1999). Except for the daily inundated zone that was only ungrazed, the three other zones (weekly, monthly and annually inundated) were divided in grazed and ungrazed zones. Cattle grazing was permanent since 1972, but infrequent and not intensive (stocking rate of 1.3–1.7 animals ha⁻¹) (Bakker, 1985). The ungrazed zone has been free of cattle since 1972, but hares could graze in both zones (in low density); the great dominance of the plant species *Elytrigia atherica* prevented from the presence of geese. The inundation gradient spanned across 1 km, with plots of each inundation frequency located about 300 m apart. The distance between grazed and non-grazed plots, which were separated by a fence, was around 15 m. In four sub-plots of 50 × 50 cm located in the corners of each plot, we collected soil fauna of three size classes (Swift et al., 1979; Decaëns, 2010) representing the most important species groups with regards to abundance: nematodes (microfauna), Collembola (mesofauna) and macrofauna (See Appendix 1 for the complete list of species and morphospecies in the different plots).

2.1. Sampling of soil fauna

Nematodes were sampled following Cobb's method (Cobb, 1918; Van Bezooijen, 2006), collecting four cores of soil in each of the seven plots with a 2 cm wide corer to a depth of 20 cm. Nematode density was estimated from two sub-samples of 5 ml taken from a 100 ml suspension of nematodes (which consisted of 100 g of soil and 100 ml of water) with a 35× magnification stereoscopic microscope. The body mass of nematodes was calculated using Andrassy's formula, based on the length and maximum diameter of nematodes for at least 20 individuals per 5 ml subsample and later averaged (Andrassy, 1956). The length and maximum diameter of nematodes were measured with 100× and 400× magnification respectively. As we were not able to identify the nematodes to species level, they were distributed into two categories (here called morphospecies), depending on their body mass: smaller than 10⁻⁷ g and larger than 10⁻⁷ g.

We sampled Collembola by collecting four 10 cm wide cores of soil in each plot to a depth of 5 cm where collembolan communities are mostly active (Berg et al., 1998). Collembola were extracted in Tullgren funnels (10 cm in diameter) for 20 days (Van Straalen and Rijninks, 1982). Identification was undertaken under a dissecting microscope based on Hopkin (2007) and the dry body masses were calculated with allometric relationships from Caballero et al. (2004), where species specific length and corresponding exponent values are provided.

Soil macrofauna was sampled using 10.5 cm wide and 12 cm deep pitfall traps without preservative in the corners of each four sub-plots per plots. We fenced the sub-plots with 50 × 50 cm Perspex boards, of which 20 cm were in the soil, to obtain a better estimate of the total abundance, preventing animals from coming in or out during sampling time. 96 traps (4 traps × 4 sub-plots × 6 plots) were open for seven consecutive days and emptied every 24 h. The traps of the daily inundated plot (4 traps × 4 sub-plots × 1 plot) were also open for seven days, but they were checked every 12 h to avoid loss of material by tidal flooding. The animals of the four traps of each sub-plot were preserved in 70% ethanol and pooled together for further analyses. After identification with a stereoscopic microscope, the animals were then dried for 24 h at 105 °C (Benke et al., 1999) before being weighted with a microscale with a precision of 1 µg. The species were identified at least up to their family, and sometimes up to genus or species levels (see Appendix 1).

2.2. Sampling of environmental variables

We measured three environmental variables that could explain differences between the soil fauna communities: elevation above sea level, soil salinity and the ratio between soil carbon (C) and soil nitrogen (N). Soil C and N content (dried for 72 h at 40 °C) were measured using a Fisons EA 1108 CHN–O analyser. Soil salinity was measured using an electrical conductivity meter. The soil samples were extracted from the top 10 cm of the organic layer using an auger (2 cm diameter) in each plot for the measurement of soil C, N and salinity. The elevation of each 2 × 2 m plot was measured using a theodolite.

Besides, three biotic environmental factors were measured: vegetation biomass, litter mass and litter C:N ratio. Litter mass is a proxy considering both the food resources and the habitat for soil fauna. Unfortunately, this proxy does not include an estimate of food quality available, but rather to the quantity. Therefore, litter and soil C:N ratios were also measured as an index of litter and soil quality (Ge et al., 2013), as it may be a determining factor for soil fauna distribution (Rushton and Hassall, 1987). Above-ground vegetation and soil surface litter were collected by hand using one 50 × 50 cm quadrat in each 2 × 2 m plot. These litter and vegetation samples were then dried at 70 °C for 48 h. The dry biomass was weighed and then expressed in g m⁻¹. Litter C and N contents were estimated using a Fisons EA 1108 CHN–O analyser. For all of the abiotic and biotic variables, one sample was collected in each of the seven 2 × 2 m plots (due to the small plot size). The data of the environmental variables are presented in the table of Appendix 2.

2.3. Statistical analyses

First, to test for the differences in animal density, total biomass and average body mass depending on inundation frequency and grazing in each sub-plot, and due to the unbalanced design (i.e., the lack of a grazed plot in the daily inundated site), we used Linear Mixed Models (LMM, e.g., McCulloch and Searle, 2000) with the inundation frequencies, grazing and their interaction as fixed factors, followed by a Sidak post-hoc test for the pairwise comparisons between the groups. A test of the normality of the residuals showed that the total biomass and the average body mass required being ln-transformed prior to computation.

We used Ordinary Least Square (OLS) regression (Reuman et al., 2008) to calculate the slopes of the DBM relationships, with data based on densities of nematodes, Collembola and macrofauna collected in the pitfall traps. We then computed the regressions and tested for differences between the slopes of the different sites by the means of ANCOVAs, i.e., GLMs with the animal densities as the dependent variable, the sites as a fixed factor, the body mass as a covariate and the interaction between site and body mass. We used the significance of the parameter estimates of the interaction in the GLMs to test the differences in slopes between the sites. To test for differences between Y-intercepts, we followed the method proposed by Zar (1996). Due to the lack of repetitions, statistics could not be performed on the environmental factors.

3. Results

3.1. Environmental variables

As could be expected, plots closer to the sea had lower elevation above sea level and higher salinity (Fig. 2A and B). Plant biomass showed a large difference between the grazed and ungrazed plots, being much higher in the latter ones, but did not show strong variations along the inundation gradient (Fig. 2C). Litter mass in the

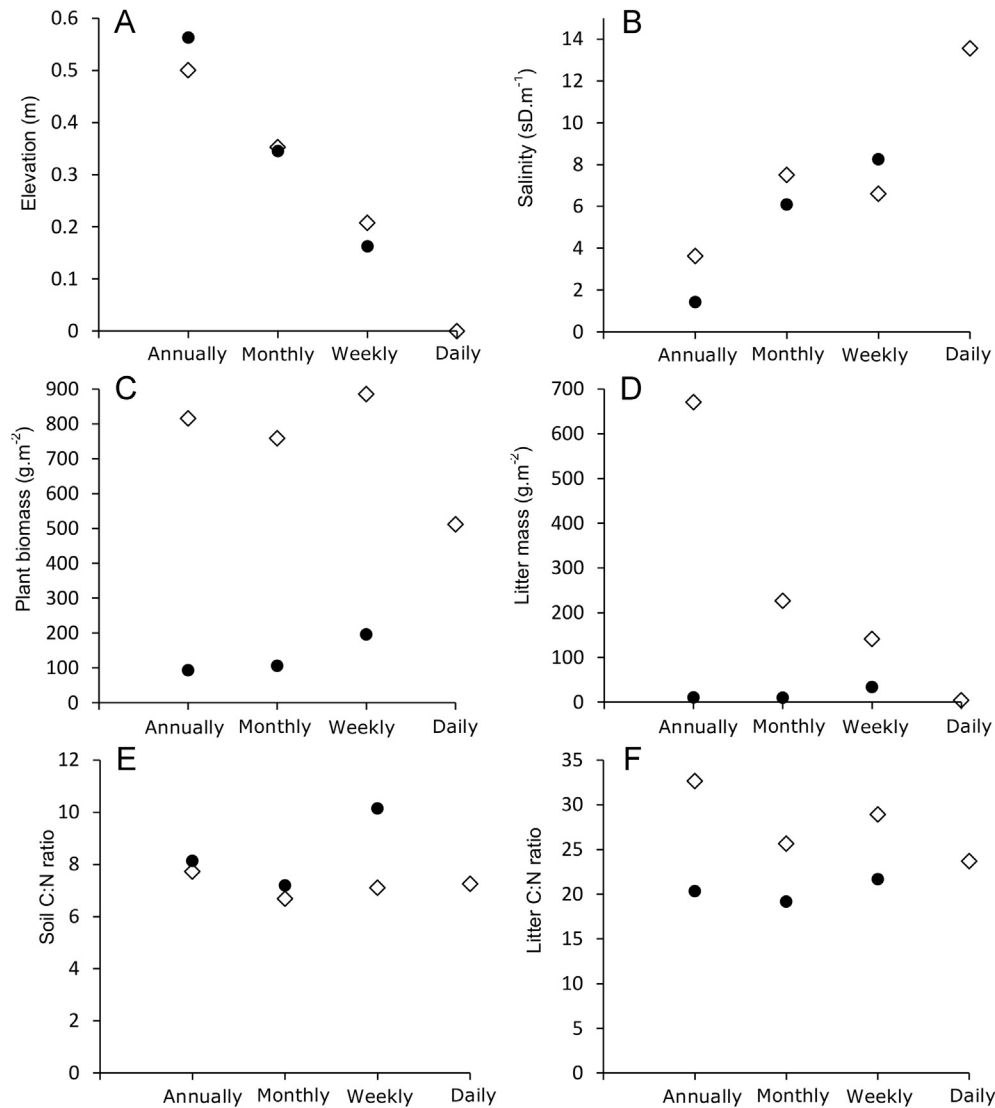


Fig. 2. Environmental variables of the grazed (●) and ungrazed (◇) plots depending on their frequency of inundation (annual, monthly, weekly and daily inundation). (A) elevation above sea level using daily inundation as the reference, (B) salinity, (C) plant biomass, (D) litter mass, (E) soil C:N ratio and (F) litter C:N ratio.

ungrazed plots strongly decreased with increasing inundation frequency and had low values in the grazed plots (Fig. 2D). Both soil and litter C:N ratios (Fig. 2E and F) showed no clear change over the inundation gradient or between grazed and ungrazed plots.

3.2. Soil fauna responses

The LMMs on the total animal density, total biomass and average body mass revealed some differences between the frequencies of inundation, both in the grazed and ungrazed plots (Fig. 3; Appendix 3, Table 1). In both the grazed and ungrazed plots, the total density of animals increased as the frequency of inundation decreased (Fig. 3A). The total biomass followed a similar pattern in the grazed plots only; this pattern was opposite in the ungrazed plots (Fig. 3B). Likewise, in the ungrazed plots, the average body mass was the highest where the frequency of inundation was the highest (Fig. 3C). In the grazed plots, there was no difference for the average body mass between the different frequencies of inundation (Fig. 3C). The total density of the annually and monthly inundated grazed communities was significantly higher than the ungrazed ones (Fig. 3; Appendix 3, Table 2). The total biomass of the grazed

plots was higher for the annually inundated communities, but lower for the monthly and weekly inundated communities. The average body mass per sub-plot was higher in the grazed plots than in the ungrazed ones when subjected to the annual inundation, but lower in the monthly and weekly inundated plots. It should be noted that the three graphs are not independent: the total density of animals of the ungrazed sites increased as the inundation frequency decreased, whereas the average body mass increased with increasing inundation frequency with similar magnitude, resulting in no differences in total biomass in the ungrazed sites subjected to different inundation frequencies.

The regressions based on the DBM relationship showed significant slopes for the communities of the grazed and ungrazed plots, except for the daily inundated one (Fig. 4A–G). We also computed the relationships obtained when omitting the two smallest groups of soil fauna (the two nematode morphospecies): then, all the slopes were much shallower and few remained significant (Fig. 4H). When considering all the animals, there were no differences between the Y-intercepts for the different inundation frequencies (One-way ANOVA: Grazed: $F_{2,65} = 0.24$, $P = 0.789$; Ungrazed: $F_{3,79} = 0.24$, $P = 0.871$) nor between the grazed and ungrazed plots

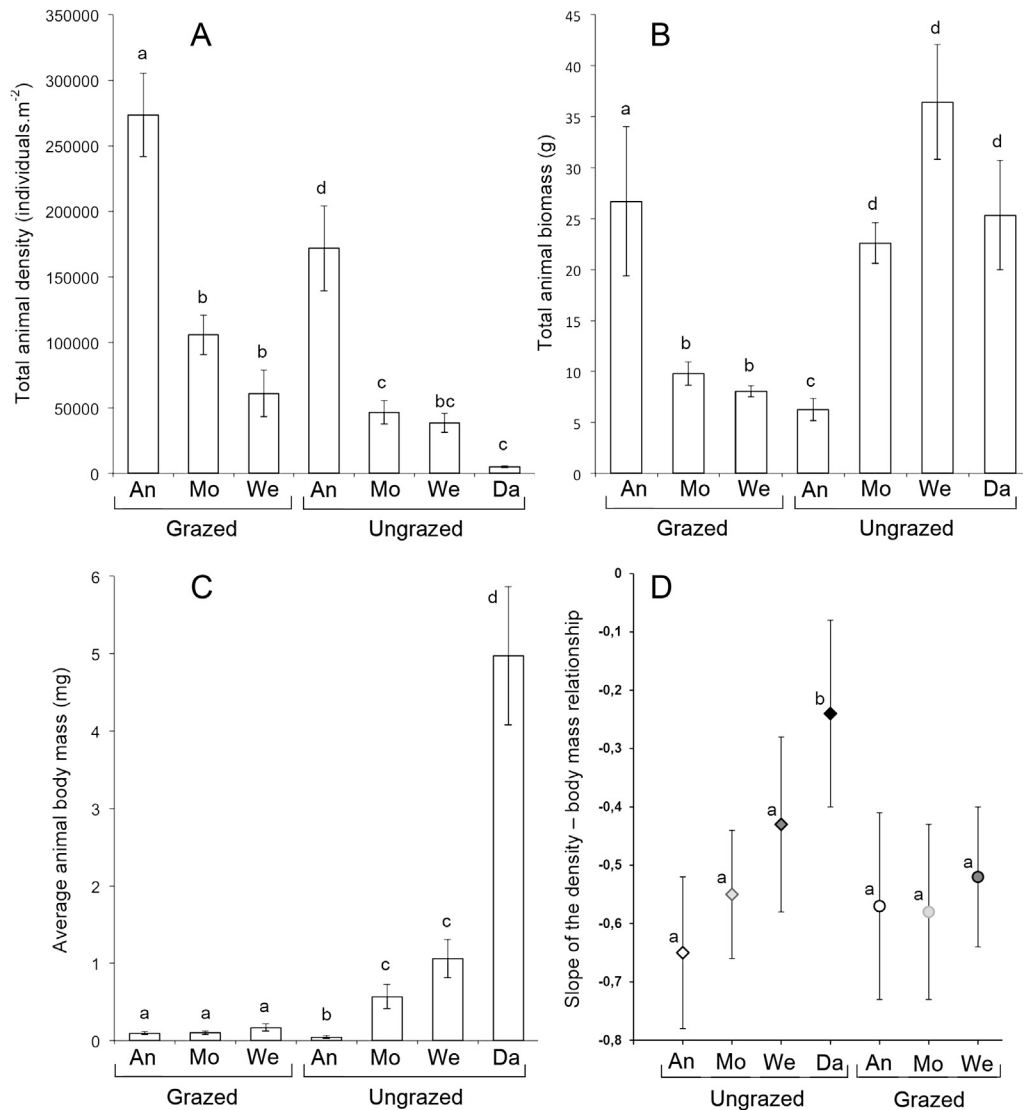


Fig. 3. Density, total biomass and average body mass of the soil fauna. Estimated marginal means (± 1 SE) of (A) the total density (number of animals per m^2), (B) total biomass (g) and (C) average body mass (mg) of the soil fauna of the ungrazed and grazed communities depending on the frequency of inundation. (D) Slopes (± 1 SE) of the density–body mass relationship of the communities. An.: annual inundation, Mo.: monthly inundation, We.: weekly inundation; Da.: daily inundation. Letters indicate differences between frequencies of inundation or grazing (not across the seven combinations of treatments).

(Annually inundated: $t_{(47)} = -0.53$, $P = 0.700$; Monthly inundated: $t_{(50)} = -0.95$, $P = 0.828$; Weekly inundated: $t_{(36)} = -0.78$, $P = 0.781$). ANCOVAs testing for differences between the slopes correlated to the frequency of inundation showed that, overall, there were no differences between the DBM relationship slopes (Table 1). However, the parameter estimate of the slope for daily inundation (the estimate for the interaction between daily inundation and body mass) differed significantly from the parameter estimate of the slope for annual inundation (the estimate for the interaction between annual inundation and body mass) (Table 2). A graph comparing the slopes of the seven communities is presented in Fig. 3D. There were no differences between the slope of the grazed and the ungrazed plots subjected to the same frequency of inundation (Table 3).

4. Discussion

In this study, we tested whether a disturbance that affects the level of productivity of ecosystems modifies animal community

structures represented by the soil fauna density–body mass (DBM) relationship. As it is based on two fundamental ecological indices, density and body mass, this relationship is expected to reflect changes in the community structure due to changes in the level of productivity and disturbances (Cyr et al., 1997a; Reuman et al., 2009). Results of studies on relationships between density and body mass have shown much discrepancy in regression slopes or distributions (Morse et al., 1988; Nee et al., 1991; Silva and Downing, 1994; Ernest et al., 2003; Russo et al., 2003; Ulrich et al., 2005; Maxwell and Jennings, 2006), if any slope at all (e.g., Gaston and Lawton, 1988). When used to detect environmental modifications due to disturbances, relationships between density and body mass also gave mixed results, some studies finding no relationship with the environment (Siqueira et al., 2008), others finding a clear relationship, though sometimes opposite (Cyr et al., 1997a; Reuman et al., 2009). In the present study, we compared the relationships of soil fauna communities over a productivity gradient (i.e., litter mass) created by seawater inundation frequency and cattle grazing.

Table 1
Results of the ANCOVAs comparing the slopes of the density–body mass (DBM) relationships of the soil fauna communities subjected to the different frequencies of inundation.

	Frequencies	Body mass	Frequencies × body mass
Grazed	$F_{2,63} = 0.1$ $P = 0.912$	$F_{1,63} = 44.6$ $P < 0.001$	$F_{2,63} = 0.1$ $P = 0.960$
Ungrazed	$F_{3,76} = 1.1$ $P = 0.350$	$F_{1,76} = 48.7$ $P < 0.001$	$F_{3,76} = 1.6$ $P = 0.198$

The bold numbers indicate the significant variables.

We used several ecological indices (i.e., the total density, the total biomass and the average body mass) to help characterizing the communities and compared them to the DBM relationships. These indices showed that in the least inundated plots of the ungrazed area, there were many soil organisms with a small average body mass, whereas in the most inundated plots, there were very few soil organisms and their average body mass was large (Fig. 3A). This suggests that, as productivity is the highest in the annually inundated non-grazed plots, represented by the high quantity of litter mass in these plots (Fig. 2D), there were more small individuals in the high productivity plots at the expense of the large ones. This agrees with Cyr et al. (1997a), who found more productive ecosystems to have proportionally more small animals, but it is contrary to what Aava-Olsson (2001) found with ground-dwelling Coleoptera in boreal forests. Therefore, our findings corroborate Hypothesis 2: in the ungrazed plots, an increase in productivity would result in a lower value of the coefficient b (i.e., a steeper slope) of the DBM relationship from the sites with annual to daily inundation (Fig. 4D–G) (Cyr et al., 1997a; Jennings and Mackinson, 2003). It must be noted that sampling a wide range of body masses was necessary to find significant slopes and detect differences between them; had we not, for instance, taken the nematodes into account, the slopes would have been shallower (higher values) and few would have been significant (Fig. 4H).

Although our sample size was relatively low (as regard to the number of plots), we found slopes varying from -0.43 to -0.65 ; as these values are higher than -0.75 , this shows that, in those soil fauna communities, populations of large animals use more energy than populations of small ones. However, even though the slopes have values differing from -0.75 , we suggest that the increase in the DBM relationship with increases in productivity indicates that the population energy use of soil fauna per unit area (the product of density and individual metabolic requirements) is not constant over a range of body masses, which contradicts the energetic equivalence rule (EER) (Nee et al., 1991). By merely looking at the relative changes of the DBM relationship, our findings suggest that the population energy use per unit area decreases as function of body mass along a gradient of productivity. As our combined sampling methods must have allowed us to sample several trophic levels, this could be explained by the less efficient transfer of energy to higher trophic levels while mostly small organisms benefit from this higher productivity (Cotgreave, 1993; Marczak et al., 2007). A typical cause of inefficient transfer of energy in soil

fauna communities is a high abundance of omnivores (Polis and Strong, 1996). In food webs, the inefficient transfer of energy through food chains creates disparities in energy availability at different trophic levels, especially if the different species do not share the same energy source and thus, increased productivity does not equally affect the different trophic levels (Cotgreave, 1993; Maxwell and Jennings, 2006; Marczak et al., 2007). This could suggest that the EER may stand for within-trophic-level comparisons, but fails for between-trophic-level comparisons.

In our study, we used litter mass as a proxy for productivity as soil fauna communities are found to increase in species richness and abundance with litter mass (Batzer and Wissinger, 1996; Lavelle, 1996; Barberena-Arias and Aide, 2003). This proxy seemed to be the most appropriate, as soil fauna from different trophic levels depend, directly or indirectly, on litter, which may serve as food (Arpin et al., 1995; Sayer, 2006), habitat (David et al., 1991) and refuge to hide from predators (Karban et al., 2013). Productivity could have been measured by the quantity of plant biomass produced per unit surface area in one year, in grams of dry matter $\cdot m^{-2} \cdot year^{-1}$ (Calow et al., 1998), but this choice implied logistical and time constraints that could not be met in this rather remote environment. Previous studies have shown that soil fauna species are specialised depending on micro-habitat (Usher et al., 1982) and that their productivity could be strongly related to the quality rather than the quantity of the litter (Batzer and Wissinger, 1996) or organic matter (Rushton and Hassall, 1987). Our data on the C:N ratios did not show much difference between the quality of the resource of the different plots, although we found differences between the structures of the communities, which may indicate that these communities were in fact more responsive to the quantity than the quality of the resource. Other factors, such as clay content and soil structure changed with inundation frequency, and these factors may have also influenced the abundance and diversity of soil fauna and vegetation (Dexter, 1988).

Regarding the influence of grazing on the communities, in the ungrazed plots, the animal total biomass was the highest in the most frequently inundated plots whereas, in the grazed plots, it was the highest in the least frequently inundated plots. Hence, this suggests that cattle grazing modified the resource availability or use from the soil fauna. We can assume that the combination of both the low productivity and the impact of grazing impeded the growth of the faunal community. However, there was no clear difference between the slopes of the DBM relationships of the grazed and ungrazed sites, therefore, the disturbance did not have the impact that we had expected. This may be due to the fact that cattle grazing decreased and induced uniformity in the litter mass across the plots despite the different frequency of inundation, which may explain why there was no difference either in the average body mass of the grazed area (Fig. 3B). Furthermore, grazing significantly decreased the vegetation height (Fig. 2C), increasing the soil's exposition to drought as well as soil compaction (Coffin et al., 1998; Schrama et al., 2012), thereby reducing the soil's pore size (Schrama et al., 2013) which may explain that the average body mass was lower in the grazed communities subjected to monthly and weekly inundation. However, pore size did not seem to be an essential environmental filter for the ungrazed

Table 2
Significance of the pair-wise comparisons of the parameter estimates for the slopes of the density–body mass (DBM) relationships of the soil fauna communities subjected to the different frequencies of inundation.

	Annually vs. monthly	Annually vs. weekly	Monthly vs. weekly	Annually vs. daily	Monthly vs. daily	Weekly vs. daily
Grazed	$P = 0.954$	$P = 0.833$	$P = 0.787$	N.A.	N.A.	N.A.
Ungrazed	$P = 0.575$	$P = 0.232$	$P = 0.486$	$P = 0.042$	$P = 0.107$	$P = 0.352$

The bold numbers indicate the significant variables.

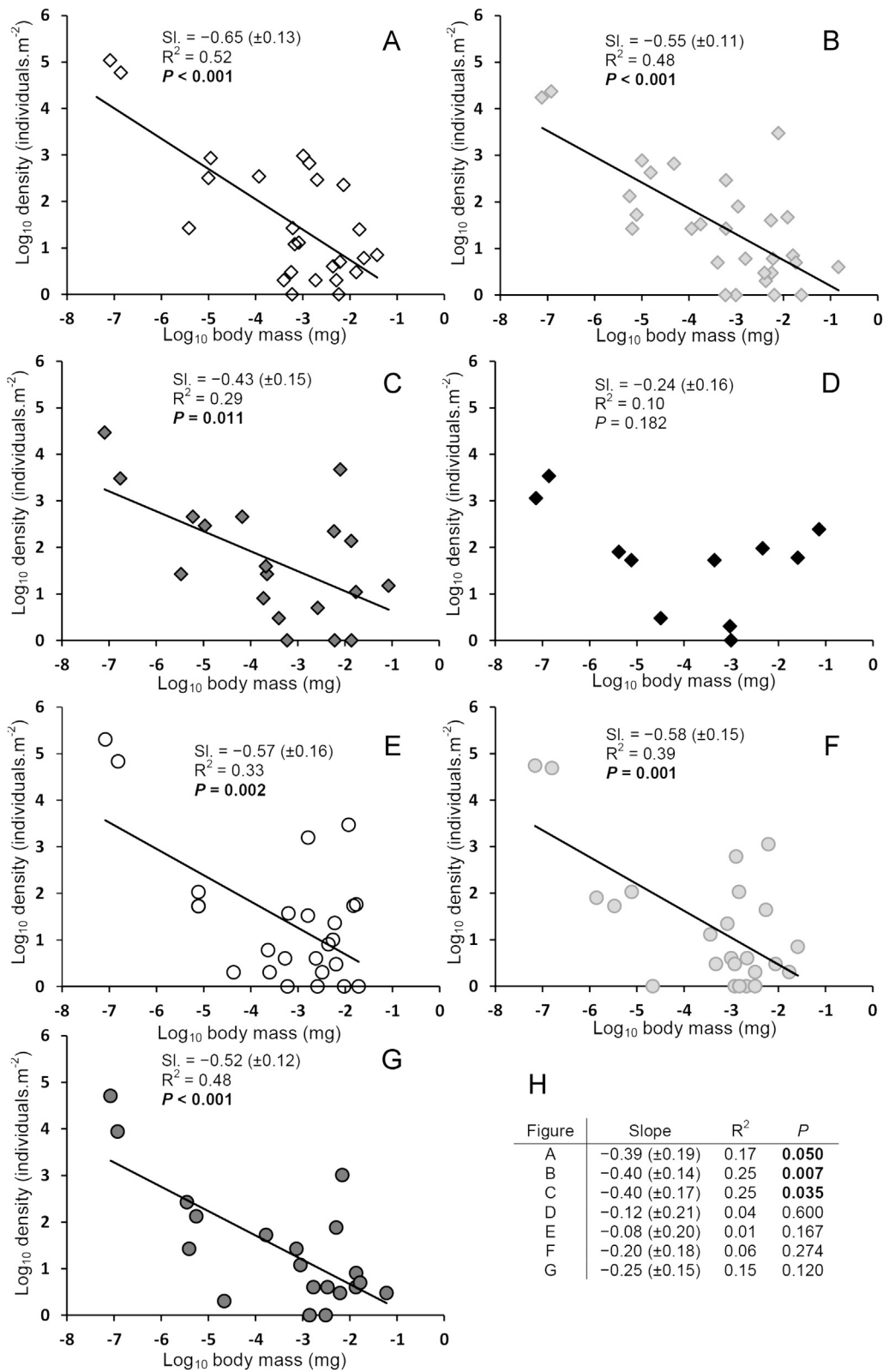


Fig. 4. Density–body mass relationships. Regressions of the density–body mass (DBM) relationships of the grazed and ungrazed plots subjected to (A, E) annual, (B, F) monthly, (C, G) weekly or (D) daily inundation and (H) table of the values of the slopes, R^2 and P when the two groups with the smallest body mass (i.e., nematodes) are omitted. Significant relationships have a trend line. SI: slope ($\pm 1SE$); R^2 : adjusted R^2 . Legend: white: annual inundation; light grey: monthly inundation; dark grey: weekly inundation; black: daily inundation; rhombi: ungrazed; circles: grazed.

Table 3
Results of the ANCOVAs comparing the slopes of the density–body mass (DBM) relationships of the soil fauna communities in the presence and absence of grazing.

	Grazing	Body mass	Grazing × body mass
Annually inundated	$F_{1,46} < 0.1$ $P = 0.866$	$F_{1,46} = 36.0$ $P < 0.001$	$F_{1,46} = 2$ $P = 0.672$
Monthly inundated	$F_{1,49} = 0.3$ $P = 0.612$	$F_{1,49} = 41.3$ $P < 0.001$	$F_{1,49} < 0.1$ $P = 0.894$
Weekly inundated	$F_{1,35} = 0.6$ $P = 0.443$	$F_{1,35} = 24.5$ $P < 0.001$	$F_{1,35} = 0.2$ $P = 0.630$

The bold numbers indicate the significant variables.

communities; even though we did not directly measure the soil structure, one can expect pore size to decrease from the least to the most frequently inundated plots (Blom and Voeselek, 1996) but instead, the average body mass increased across the same gradient. Therefore, it seems that the size structure of soil fauna communities is not determined by soil structure (i.e., pore size) but rather by other factors, like had been shown in studies carried out in marine and freshwater environments (Duplisea and Drgas, 1999; Seiderer and Newell, 1999). Our results suggest that productivity was more important for the size distribution of the communities than the effects of cattle grazing and seawater inundation on soil structure.

5. Conclusion

The relationship between soil fauna's density and body mass is an energetic relationship that can provide information on the size structure of a community (body mass distribution) as this is a reflection of the energy use of the different body mass categories, showing the main resource consumers of the community (Nee et al., 1991). However, it requires a thorough sampling of a wide range of body masses and strong relationships to be able to detect the effects of environmental variations from one community to another, as these variations appear quite subtle at the community level (Cyr et al., 1997a). With the use of the DBM relationship, we were able to detect differences between similar soil fauna communities living in environments of various productivities. Productivity, which was measured through the proxy litter mass, did not seem to influence the average body mass of soil fauna, but it may rather have modified the structure of the soil fauna communities (De Deyn and van der Putten, 2005) by affecting the smallest animals only; thus, the communities from low productivity areas seemed to be unbalanced because of the lack of small organisms. Our findings were supported by simple ecological indices such as the total density, total biomass and average body mass, except for the effect of grazing.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.soilbio.2014.02.003>.

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