Soil Biology & Biochemistry 78 (2014) 30–37

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

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

Disturbance–diversity relationships for soil fauna are explained by faunal community biomass in a salt marsh

Madhav Prakash Thakur [a, b, *, 1, 2], Matty P. Berg [c, d], Nico Eisenhauer [b, 1, 2], Frank van Langevelde [a]

[a] Resource Ecology Group, Wageningen University, Droevendaalsesteeg 3a, 6708 PB Wageningen, The Netherlands
[b] Institute of Ecology, Friedrich Schiller University Jena, Dornburger Str. 159, 07743 Jena, Germany
[c] Department of Ecological Science, Section Animal Ecology, VU University, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands
[d] Centre for Ecological and Evolutionary Studies, Community and Conservation Ecology Group, University of Groningen, Postbox 11103, 9700 CC Groningen, The Netherlands

ARTICLE INFO

Article history:
Received 3 January 2014
Received in revised form
10 June 2014
Accepted 29 June 2014
Available online 3 July 2014

Keywords:
Soil invertebrate fauna
Salt marsh
Intermediate disturbance hypothesis
Feeding guilds
Orchestia gammarellus

ABSTRACT

Disturbance–diversity relationships have long been studied in ecology with a unimodal relationship as the key prediction. Although this relationship has been widely contested, it is rarely tested for soil invertebrate fauna, an important component of terrestrial biodiversity. We tested disturbance–diversity relationships for soil meso- and macrofauna in a salt marsh where periodic sea water inundation and cattle grazing occur as stressors. We hypothesized a unimodal inundation frequency–diversity relationship, whereas we expected grazing to overrule the effects of inundation frequency due to its large effects on the habitat of soil fauna. We found a negative relationship between inundation frequency and diversity at the ungrazed sites and no relationship at the grazed sites. Moreover, we found a negative relationship between community biomass and diversity for soil fauna that may have caused this negative disturbance–diversity relationship. Community biomass at the intermediate inundation frequency increased due to the dominance of *Orchestia gammarellus* (a macro-detritivore species), which could exploit low quality litters at the ungrazed sites. We highlight that the negative relationship between faunal community biomass and faunal diversity may influence disturbance–diversity relationships and illustrate that total biomass distribution of feeding guilds of soil fauna can improve our understanding of the soil fauna response to stressors in salt marshes.

1. Introduction

Disturbances have long been argued to contribute directly and indirectly to species diversity (Kolasa et al., 1989; Maarel, 1993; Buckling et al., 2000). In general, it has been suggested that intermediate levels of disturbances or stress, both in terms of frequency and in intensity, maximize biodiversity, the so-called Intermediate Disturbance Hypothesis (IDH) (Connell, 1978; Huston, 1999; Wilkinson, 1999; White and Jentsch, 2001; Dos Santos et al., 2011). However, the proposed unimodal relationship between environmental disturbance or stress and diversity as suggested by the IDH is often not supported by empirical studies (Mackey and Currie, 2001; Hughes et al., 2008; Fox, 2012). The deviations from the unimodal relationship between disturbance and diversity have been attributed to several factors, such as site conditions, species traits, as well as the frequency and magnitude of the disturbances (Wootton, 1998; Sheil and Burslem, 2003; Shea et al., 2004). Hence, the need for studying the factors that can cause deviations from unimodal disturbance–diversity relationships has been stressed (White and Jentsch, 2001; Shea et al., 2004; Haddad et al., 2008).

Several mechanisms underlying the unimodal relationship between disturbance and diversity have been postulated. One general assumption is that long-living species are not able to thrive in highly disturbed sites, whereas colonizer species, such as *r*-strategists, in less disturbed sites are outcompeted by competitively superior species (Shea et al., 2004). Both long-living and colonizer species are however expected to co-exist in between these extremes, therefore resulting in higher biodiversity at intermediate disturbance levels (Connell, 1978; Zobel, 1997; Martin, 2001; Shea et al., 2004). Mechanisms that promote co-existence among

* Corresponding author
E-mail address: madhav.thakur@idiv.de (M.P. Thakur).
[1] Present address: German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany.
[2] Present address: Institute for Biology, University of Leipzig, Johannisallee 21, 04103 Leipzig, Germany.

http://dx.doi.org/10.1016/j.soilbio.2014.06.021
0038-0717/

species may also depend on factors like species' ability to utilize and partition resources (Buckling et al., 2000; Shea et al., 2004; Haddad et al., 2008). The ability of species in communities to utilize and partition resources is often reflected in the net productivity of the communities or the community biomass (total biomass of the co-occurring species within a community) (Post and Pedersen, 2008). Fluctuations in community biomass may provide explanations for the variations in disturbance–diversity relationships (Gough et al., 1994; Huston, 1994; Kondoh, 2001). For instance, the increase in the community biomass due to an increase in dominant species in the absence of disturbance may shift the community composition and thus decrease species diversity (Kondoh, 2001). Moreover, local environmental conditions such as habitat and resource heterogeneity in case for soil fauna could equally determine soil fauna diversity (Decaëns, 2010). The extent to which disturbances may alter local environmental conditions therefore is crucial to understand how much disturbance could influence local species diversity.

In this study, we analyze how the diversity and biomass of soil fauna communities change in the presence of two distinct types of stressors in a salt marsh: sea water inundation (physical stress) creating an abiotic stress gradient in terms of inundation periodicity and salinity, and cattle grazing (abiotic and biotic stress) creating differences in vegetation and leaf litter biomass, available soil pore space and redox potential of the soil (Schrama et al., 2012). Along the stress gradient in a salt marsh, intermediate disturbance is likely to be found spatially in between highly stressed sites that are very frequently inundated with salt water, such as every day or every week, and in less frequently inundated sites with low stress levels, such as inundated once every year due to very high tides (Hacker and Bertness, 1999). Salt marshes have distinct vegetation zones due to this variation in periodic inundation (Olff et al., 1997), and they are also characterized by the presence of numerous soil fauna species varying in their density along the inundation gradient (Hacker and Gaines, 1997; Schram et al., 2012).

The soil fauna living in the sub-surface of the soil in salt marshes face regular abiotic stresses in terms of salinity and anoxic conditions by the periodic sea water inundation (Hacker and Gaines, 1997; Pennings and Bertness, 2001). Regular inundation can increase the mortality of some species (Evin and Talley, 2002), whereas other species are adapted to salinity and survive inundation for some duration (Witteveen and Joosse, 1987). For example, salinity-intolerant soil fauna are higher in density in more elevated parts of the salt marsh where inundation frequency is low (Pennings and Bertness, 2001; Ellers et al., 2010), while salinity-tolerant species are often absent at high elevation parts because they are outcompeted by intolerant species as salinity and anoxia tolerance comes at a cost. Essentially, due to differences in adaptation, diversity of soil fauna has been suggested to vary with the frequency of sea water inundation in salt marshes (Hacker and Gaines, 1997; Pennings and Bertness, 2001).

Cattle grazing in some salt marshes has historically been introduced as a management practice to improve livestock health, such as in the salt marshes of the Wadden Sea in the Netherlands (Bakker, 1985), and as a nature conservation approach to reduce the presence of the grass species *Elytrigia athericus*. The parts of salt marshes that are grazed by cattle have a short vegetation height and low leaf litter biomass (Andresen et al., 1990; Bos et al., 2002; Wu et al., 2009). It is therefore likely that litter-feeding soil fauna have low densities in grazed sites due to reduced aboveground resource inputs (Andresen et al., 1990). Moreover, soil fauna in grazed sites is more exposed to light, with usually lower soil moisture content, higher temperatures, and stronger diurnal fluctuations in microclimate compared to ungrazed sites due to short vegetation (Andresen et al., 1990). Cattle grazing also changes soil characteristics that increase the susceptibility of nutrient losses through water erosion (Neff and Reynolds, 2005), and trampling of fine-textured soil by cattle results in significant soil compaction, reduction in soil porosity and locally anoxic conditions (Schrama et al., 2012). All these effects of grazing together might result in lower soil fauna biomass in grazed sites compared to ungrazed sites (Andresen et al., 1990; Schrama et al., 2012). Moreover, grazed and ungrazed sites may differ in the composition of feeding guilds in the soil. For example, ungrazed sites have been found to be dominated by litter feeding macro-detritivores, whereas invertebrate herbivores are generally higher in density in the grazed sites of salt marshes (Andresen et al., 1990; Schrama et al., 2013).

According to the intermediate disturbance hypothesis, we hypothesize soil fauna diversity to peak at the sites with an intermediate sea water inundation frequency, i.e. every month, which is intermediate between annual and daily/weekly flooding at the high and low elevation end of the gradient, respectively (hypothesis 1). Further, we hypothesize that cattle grazing will overrule the effects of inundation frequency on soil fauna diversity due to its large effects on the habitat of soil fauna (hypothesis 2). We also test the community biomass-diversity relationship for soil fauna at both cattle grazed and ungrazed sites along the inundation gradient and show that this relation may help explain patterns observed for the disturbance–diversity relation. We finally illustrate total biomass of soil fauna of key feeding guilds on the inundation gradient and in response to cattle grazing to highlight soil fauna responses to stresses and subsequent effects on soil fauna diversity.

2. Material and methods

2.1. Study sites

The study area was located on the salt marsh of Schiermonnikoog, a barrier island in the Wadden Sea, the Netherlands (53°28′43N, 6°14′06 E). The field study was carried out from October to November 2011. Seven sites were selected based on inundation frequency, in an area with and without cattle grazing (Table 1, see also Comor et al., 2014). We selected sites that were characterized by daily inundation, weekly inundation, monthly inundation and yearly inundation, representing the low, lower-middle, upper-middle and elevated parts of the salt marsh, respectively (Hacker and Bertness, 1999). The exact locations of the sites were based on the thickness of the clay layer, as clay depth indicates inundation frequency in this salt marsh and separates intertidal zones (Olff et al., 1997; Schrama et al., 2012). Except for the daily inundated site, we selected at each inundation frequency two sites with similar thickness of the clay layer: one with and one without cattle grazing (grazing intensity: 1.6 animals/ha, Bakker, 1985). In the area that inundated daily no cattle were allowed. The ungrazed sites were separated from the grazed sites by an electric fence.

2.2. Soil fauna collection

We collected soil mesofauna and macrofauna species, two dominant groups on this salt marsh (Schrama et al., 2012; Comor et al., 2014). The selection of these two soil fauna groups represents a large proportion of soil animals in terms of their feeding interactions and body size variation (Decaëns, 2010). The mean body sizes of the soil macrofauna, comprising invertebrates such as Coleoptera and Mollusca, ranged from 2 mm to 20 mm, whereas mesofauna, such as Collembola, ranged from 100 μm to 2 mm (Decaëns, 2010). For the mesofauna, we only included Collembola, which is the most dominant mesofauna group in the study area (Schrama et al., 2012). We studied soil mesofauna and macrofauna