Disturbance and recovery of litter fauna: a contribution to environmental conservation

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Propositions

1. The environmental filters created by constraining environmental conditions may influence a species assembly to be driven by deterministic processes rather than stochastic ones.
   (this thesis)

2. High species richness promotes the resistance of communities to disturbance, but high species abundance does not.
   (this thesis)

3. The risks generated by nanotechnologies will contribute to making people more sceptical about the benefits of science.

4. The concept of ecosystem services denies the intrinsic value of nature in favour of its utilitarian value.

5. Social media do not make the detection of social tipping points more effective in predicting societal upheavals.

6. Any ethical reflection ventures into normative thinking.

Πάντα ῥεῖ [1]

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[1] Panta rhei, everything flows

Table of contents

CHAPTER 1

Disturbances have long been studied in ecology (Cooper 1926; Watt 1947; Lull 1959; Mathisen 1968; Dayton 1971) and their impacts have been described for even longer (Pliny the Younger 1963), because of the detrimental consequences they can have on human populations. The range of action of disturbances in time and space spans from almost insignificant, suczh as a footstep in the forest, to floods (e.g., Yount and Niemi 1990), oil spills (e.g., Piatt et al. 1990), fires (e.g., Turner et al. 2003), volcanic eruptions (e.g., Franklin and MacMahon 2000) and meteorite impacts (e.g., Pope et al. 1998).

The importance of disturbances for the functioning of ecosystems has been shown in many studies (e.g., Levin and Paine 1974; Wootton et al. 1996; Hubbell et al. 1999; Bengtsson et al. 2000), which also pointed out several factors that can mediate the outcome of a disturbance. The frequency, intensity and duration of a disturbance have an influence on an ecosystem's ability to resist and recover from a disturbance (Sousa 1984). For instance, nearby communities undergoing a frequent disturbance will tend to have very similar composition and structure, whereas seldom disturbed communities may be relatively different from each other (Chase 2007). Besides the characteristics of a disturbance, the structure of a community is known to affect resistance and capacity of recovery: for instance, a species-rich or diverse community (in terms of life-history traits) is predicted to better resist and recover from a disturbance than a low-richness community. This phenomenon has been named the insurance hypothesis (Naeem and Li 1997). The environmental conditions in which a disturbance occurs can also strongly influence the recovery of a community, and a highly productive system is thought to allow for a much less deterministic re-establishment (i.e., more random and unpredictable) (Chase 2010). Therefore, the combination of the characteristics inherent to the disturbance, the community and the environment may lead to dramatically different outcomes after an ecosystem has recovered. However, the synergetic effects of these determinants on the outcome of a disturbance are not known yet.

The negative impacts disturbances can have on natural and anthropogenic systems can lead to the collapse of an ecosystem (Jackson et al. 2001; Scheffer et al. 2001), but it has also been shown that disturbances can have positive consequences for ecosystems (Connell 1978). These usually involve an increase in species richness and/or a higher stability, allowing these systems to better resist future disturbances (McIntyre et al. 1988; Nyström et al. 2000; Van Auken 2000). The recovery ensuing a disturbance can thus lead to different (yet stable) communities from the ones preceding the disturbance and it appears relevant to understand the mechanisms of recovery to be able to predict the possible structures of communities following a disturbance. Difficulties to make predictions have already been expressed (Prins and Gordon 2013), as recovery is the product of idiosyncratic characteristics pertaining to each disturbance, site and community (Power 1999). Understanding recovery seems a prerequisite for the long-term protection and management of natural, as well as anthropogenic, ecosystems (Dobson 1997; Scheffer et al. 2001; Brudvig 2011), especially as restoration ecology is becoming an important field of conservation (Dobson 1997; Young 2000). However, although disturbances have been thoroughly studied for the last decades, the recovery of communities following a disturbance is seldom the main focus of studies (Figure 1), mostly because of a lack of time and budget (Niemi et al. 1990).

This thesis focuses on the interaction between disturbance characteristics, environmental characteristics and community characteristics. It is based on a series of experiments in which I monitored the ensuing recovery of different soil and litter fauna communities after a disturbance using several ecological indices. I also tested the ability of a well-known ecological relationship linking density and body mass to reflect the structure of communities impacted by a disturbance and their subsequent recovery. Finally, I used this relationship to assess the different structures of communities subjected to disturbances and different levels of productivity. After defining disturbance and recovery in the next section, I will introduce the main ecological concepts used in the different chapters of this thesis, especially with regard to soil and litter fauna communities.

Definition of disturbance

The definition of disturbance in ecology is not always clear and has raised many discussions (Sousa 1984, 2001; Pickett and White 1985; Rykiel 1985; Pickett et al. 1989; Walker and Willig 1999; Mackey and Currie 2000). This is understandable as very few systems are absolutely undisturbed (Connell and Sousa 1983) and, if one defined a disturbance as any modification of an environmental variable, such as changes in temperature or light, then it could be argued that night vs. day or winter vs. summer are disturbances. Therefore, only a few places on Earth could be considered as undisturbed, i.e., with constant environmental conditions, such as the 35 million-year old, 4000-metre below the surface Vostok Lake (Schiermeier 2010). Such a narrow definition and extreme example do not apply to what I will hereafter consider as undisturbed ecological systems. On the other hand, though some authors may consider a fire as non-disturbing because it is part of the natural course of some systems (Rapport et al. 1985), the definition that I propose does not agree with this statement.

In this thesis, a disturbance is defined "as an event that is massively destructive and rare" (Rykiel 1985) and that reduces the living biomass. Sousa (1984) defined a disturbance as "a discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established". Therefore, an important characteristic of a disturbance, regardless of its positive or negative impact on the ecosystem, is the decrease in biomass it causes, either immediately or in the long run. The definition can be completed by Mackey and Currie's input (2000) that states that a disturbance is "a force often abrupt and unpredictable, with a duration shorter than the time between disturbance events, that kills or badly damages organisms and alters the availability of resources". The unpredictability of disturbance (Wingfield 2013) is relevant as it excludes circadian and seasonal cycles, but includes events such as fires or floods. A disturbance should also be defined relative to the subject of interest and the qualification of an event as disturbance depends on the hierarchical level taken into consideration (Pickett et al. 1989). Whether an event occurs at the level of a population, a community or an ecosystem and whether it concerns, for instance, only the autotrophs, the herbivores or the predators, will determine whether it is considered as a disturbance, depending on what the observer defines as the subject of interest. Moreover, the observer should define a state of reference (a benchmark) of the studied system, with what the ranges of normal environmental conditions are (e.g., minimum and maximum annual temperatures, precipitation, wind, noise, levels of chemicals, etc.), to be able to define an event as a disturbance (Rykiel 1985). Disturbances can be furthermore qualified as either endogenous or exogenous (Bormann and Likens 1979). Endogenous disturbances result from an internal event within the system into consideration, such as the fall of a dead or old tree; they are, according to Bormann and Likens (1979) "an integral part of the developmental process of an ecosystem". Exogenous disturbances, on the other hand, originate from outside of the system taken into account, such as hurricanes, fires (Bormann and Likens 1979), invasive species (Simberloff and Holle 1999) or chemical spills (Walker and Willig 1999). However, determining whether a disturbance belongs to one or the other category is sometimes difficult, if not impossible (Sousa 1984; Pickett and White 1985). This definition of disturbance corresponds to the disturbance I used in Chapter 2, 3 and 4, in which I study the consequences of a destructive one-time event on soil and litter fauna communities.

Another ecological phenomenon impeding a system's development and sometimes confused with disturbance is ecological stress. It usually is a long lasting phenomenon, hence not characterised as an event, and can become part of the environmental conditions of a system, such as a high salinity, altitude, noise, cattle trampling, heat and dryness, etc. (Wingfield 2013). At first, stress is tolerable by the organisms experiencing it; it may just inhibit their growth and induce a higher metabolic cost to their development (Wootton 1998; Sousa 2001), but its duration and/or its intensity may decrease their life span and even cause direct death (Odum 1985). In Chapter 5, I study the effects of a stress (sea inundation frequency) in combination with cattle grazing, which can be considered in the studied area as a disturbance due to its infrequent nature.

Besides the negative effects of killing individuals and removing living biomass, disturbances can have positive consequences for ecosystems, creating opportunities for recruitment (Collins et al. 1995; Huxham et al. 2000), which may increase an ecosystem's diversity and stability, at least temporally (Frank and McNaughton 1991). Several hypotheses have been proposed, based on this effect of an increase of diversity due to disturbance. However, these hypotheses, such as the intermediate disturbance hypothesis (Connell 1978) and the diversity – stability hypothesis (MacArthur 1955), are highly debated, despite the manifold studies on the topic, as empirical evidences and theoretical models have both given contradictory results (McCann 2000; Fox 2013). Controversies also exist in the management of disturbed ecosystems, for instance in fire- or flood-prone environments, as to whether areas that used to burn or be flooded naturally should still be subjected to these disturbances, because these disturbances can be dangerous (causing potential injury or death) to human populations while maintaining ecosystems and release or store greenhouse effect gases, such as CO_2 or CH_4 (e.g., Schulz et al. 2011; van Wilgen et al. 2012). Knowledge on disturbances and their consequences is not complete and this could be detrimental for nature conservation and management, as disturbances play a central role (either beneficial or detrimental, or both) in ecosystem functioning (White 1979; Pickett et al. 1989).

With the expansion of human activities, more and more disturbances have anthropogenic origins. The relative importance of these disturbances has even led Eugene Stoermer to coin the (now widely accepted) term Anthropocene to refer to the geological epoch during which humans have been active (Zalasiewicz et al. 2008). These anthropogenic disturbances affect natural environments and human populations, and their scale, frequency and severity have dramatically increased over the last centuries (Richmond 1993; Vörösmarty and Sahagian 2000). Therefore, understanding how they occur as well as their consequences has become a relevant and critical field of research for our modern societies, with the aim of protecting, firstly, human populations and activities, then, natural environments. Whilst the former aim can help saving lives and money, the second can contribute to saving plants and animals, and preserving landscapes.

As disturbances concern a broad scale both in space and in time and can potentially occur anywhere and at any time, they cannot infinitely be avoided (especially natural ones). Thus, focus has been directed in understanding the mechanistic actions of disturbances in order to be able to predict them as accurately as possible (e.g., Iguchi et al. 2012; Jie and Guangmeng 2013). However, there has been little attention dedicated to the recovery following disturbances, as illustrated by Figure 1. This graph shows that there has been a marked interest for issues related to disturbances in the fields of ecology and environmental sciences arising in the 1990s, peaking in the middle of the 2000s, levelling off afterward at about 2.6% of the articles published in the aforementioned fields. Research focussing on both disturbance and recovery began much later than research on disturbance only. It started very slowly in the late 1980s, rising a bit in the 1990s but never gaining much interest, as it quickly levelled off at about 0.25% of the ecology and environmental sciences articles, and has not increased since.

There is a clear lack of interest for the recovery process related to disturbance, though, as disturbances are inevitable, knowledge on the recovery is essential to tackle issues such as which species would re-establish after a disturbance (and how and why these ones), which species are necessary for the return of the ecosystem to the state

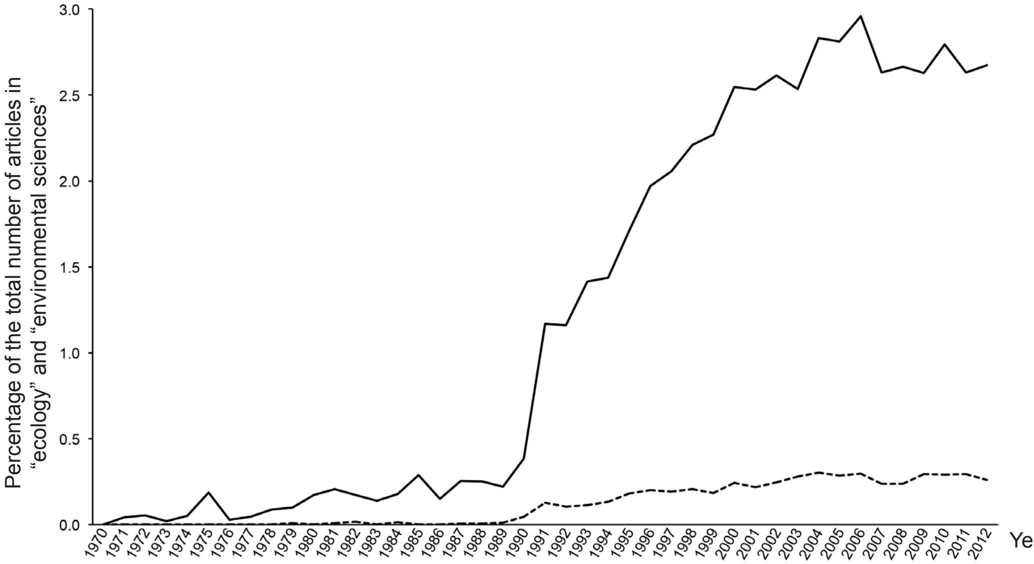

Figure 1: *Percentage of the number of scientific publications (articles, books, proceedings, etc.) containing the word "disturbance" (continuous line) or the words "disturbance" and "recovery" (dashed line) in their topic in the two categories "ecology" and "environmental sciences" compared to the total number of articles of these two categories, from 1970 to 2012, using Web of Science's search engine.*

prior to the disturbance, how long this would take, whether restoration (i.e., human intervention) is required to facilitate the recovery, etc.

Recovery in ecology

The main issue that ecologists have to deal with when considering recovery is how to define it (Parker and Wiens 2005). This is obviously highly relevant as it is necessary to be able to tell whether a system has recovered or not. Recovery is the process following a disturbance, when plant and/or animal populations start growing again (Gårdmark et al. 2003), either from the organisms that survived the disturbance or from new comers who benefited from the newly available space. This process can only start if the abiotic and biotic conditions are suitable again (Palmer et al. 1997). It is usually defined as the return to pre-disturbance steady state (Power 1999) through the different succession stages of the system dynamics (O'Neill 1999). This definition implies that recovery could be a finalistic process, thus inferring that there are climax communities toward which disturbed communities will return after any deviation from the pre-disturbance state (Clements 1916, 1936). The ecological concept of climax, even though only used to describe the succession stages of flora, not fauna, has been very controversial for almost a century (Gleason 1926; Whittaker 1951; Rull 2012). Since then, studies have shown that, after a disturbance, communities may switch to an alternative stable state (Lewontin 1969; May 1977; Case 1990; Scheffer et al. 1993, 2001; Rietkerk et al. 1996; Beisner et al. 2003; Ives and Carpenter 2007) or, conversely, that stochastic disturbing factors can allow for the persistence of an ecosystem in what appears as a non-equilibrium, preventing it from switching to another state (Jeltsch et al. 2000). In this alternative state, the structure of communities differs from the pre-disturbance state either in terms of species abundance, species richness, life-history traits or all of these ecological indices. Communities can also recover with a similar functional structure to the pre-disturbance state, but with a different taxonomic structure (different species sharing similar life-history traits (Naeem 1998)). Therefore, the questioning on the definition of recovery is in fact rooted on the mere issue of the definition of community, as the latter can slightly change over time without any disturbance (Jacobson and Grimm 1986; Sprugel 1991; Inouye 1995; Jackson and Sax 2010) and switch to an alternate state. One could then first wonder whether this is still the same community, as it can be composed of different species and functional traits, and then, how different from another state a community should be to be called alternative (Beisner et al. 2003). In this thesis, I will consider an animal community as recovered when it has returned to a structure close to its conditions prior to disturbance (National Research Council 1992), i.e., to the structure and composition it should have if it had not been disturbed (Parker and Wiens 2005).

The fact that recovery can lead to alternate states to the one preceding the disturbance is the reason why understanding recovery is essential for successful habitat conservation, restoration and management (Chapin et al. 1996). Like the definition of disturbance, the definition of recovery usually depends on the hierarchical level of the ecosystem the observer focuses on (e.g., individual, population, community, ecosystem) and, even when focussing on the same level, several measures and tools can be used to estimate recovery. For instance, in this thesis, even though all the chapters dealing with recovery (i.e., chapter 2, 3 and 4) focus on the community level of the ecosystem, a different index was used in each of the chapters; I either created a new index (Chapter 2), adapted one to fit the data (Chapter 3) or used one for the first time in this context (Chapter 4).

Besides the characteristics of a disturbance (intensity, frequency, duration, etc.), the environmental conditions (such as climate), along with the abundance and life-history traits of organisms are predicted to have far reaching implications for the recovery processes (Whitlatch et al. 1998). Therefore, during the initial stage of recovery, re-establishment of species is defined by the niche of these species (allowing them to fit in the environment, based on their life-history traits). Besides, stochasticity also occurs in the recolonization of disturbed ecosystems, as there is no competition and plenty of newly available habitats (May 1975). These two possible ways of re-establishment have led to two opposite theories to explain species assembly in community ecology: the niche theory (Chase and Leibold 2003) and the neutral theory (Hubbell 2001).

The niche theory appeared with Hutchinson's ecological niche concept, which stipulates that species assemblages mainly depend on the resources they require to develop (Hutchinson 1957). Besides those influences of the environment (and its resources) on species, the niche theory also considers the impact species have on their environment, through their consumption of resources (Vandermeer 1972). Thus, if several species depend on the same resource, there will be competition between these species, until the one that can survive with the lowest amount of this resource excludes the other(s); this competitive exclusion is a basis of the niche theory, emphasizing the role of species life-history traits. The niche theory stipulates that species coexistence and abundance depend on the reciprocal interaction species have with their environment and with other species. Therefore, interactions like competition, predation, mutualism or parasitism are important factors determining whether a given species can establish and live in a system.

On the other hand, the neutral theory supposes that differences between species are not relevant in explaining their occurrence and relative abundance; species in a community, from the same trophic level, are "ecologically equivalent" and they have equal fitness over all environmental conditions (Holyoak and Loreau 2006; Leibold and McPeek 2006). This means that species life-history traits are not relevant regarding the stochastic individual variation of fecundity, mortality and immigration within dispersal-limited systems (Hubbell 2001). Therefore, there is no competitive exclusion in systems whose species distribution can be explained by the neutral theory. Neutral theory excludes predator-prey, parasite-host and mutualistic relations, including only species with similar ways of life and competing with one another for resources (Bell 2001).

Both niche and neutral theories are used to explain species assembly and this has led to a large debate in community ecology (Stanley Harpole and Tilman 2006; Adler et al. 2007). While niche theory stipulates that species capable of colonizing a new area are those whose ecological niche allows them to live in this environment with the other species, neutral theory is based on subsequent random colonization of species, regardless of species interactions (Bell 2001). These theories have different predictions for the recovery of ecosystems. Community composition can be more easily predicted in the case of a recovery explained by niche theory, as it should be rather similar to the pre-disturbance community and to the surrounding communities subjected to similar environmental conditions. In the case of a community structure explained by neutral theory, the outcome of a recovery is hardly predictable because of the randomness involved. These communities may therefore be different from the preceding ones and from the surrounding ones too (Chase 2007, 2010). As different levels of productivity affect the composition of communities (in terms of species abundance and richness) (Wright et al. 1993) as well as the ability of species to re-establish (a low productivity could be compared to a harsh environmental filter), I compared the species assembly (after a disturbance) of similar animal communities in an experiment in contrasting biomes to test whether one theory could rather explain the structure of the recovered communities depending on the environmental conditions (Chapter 3).

Productivity and community structure

The productivity of ecosystems is thought to determine ecosystem characteristics and to affect the composition and structure of plant and animal communities (Evans et al. 2005; Gillman and Wright 2006). Overall, as productivity increases, species abundance and richness are also expected to increase, following the species – energy hypothesis (Wright et al. 1993). Thus, an ecosystem with a higher net primary productivity can support more individuals, therefore, more species as well. As the insurance hypothesis (Naeem and Li 1997) states that species-rich communities can better resist and recover from a disturbance (Frank and McNaughton 1991; Tilman and Downing 1994), due to their higher diversity and redundancy of traits (Naeem et al. 1999), the level of productivity of a community may have a dramatic impact on the outcome of a disturbance, as it determines species richness and abundances.

The causes of the level of productivity of a system can be multiple, at various scales. At a global scale, the energy the Earth receives from the sun increases from the poles toward the (thermal) equator. One consequence is that systems near the equator have been shown to be more productive (provided they are not limited by water or nutrients availability, for instance). These systems also exhibit higher species richness and abundance (Cardillo 2002; Hillebrand 2004), whether this is related to their higher productivity or not (Rohde 1992; Waide et al. 1999). Thus, I located my experimental plots in areas of different latitudes and contrasting climates to investigate the effects of varying productivity, species richness and species abundance on the recovery of communities after an equal disturbance, and I tested whether some particular life-history traits were more important in one biome than in the other for this recovery (Chapter 2).

At a much smaller scale, various levels of productivity may also originate from different stress intensities within one ecosystem. Productivity in ecosystems subjected to stress is lower and resources are usually less abundant than in non-stressed systems (Odum 1985). A lower productivity is usually caused by one or a combination of several factor(s), such as a recurrent flooding, trampling, the lack or excess of a chemical element (Rapport et al. 1985). In my thesis, I also studied the effect of the level of productivity caused by stress (i.e., sea water flooding) on the structure of communities in disturbed (cattle grazing) and undisturbed sites (Chapter 5).

Study species

Throughout the various studies of this thesis, the same group of biological indicators was used: soil and litter macrofauna. This group has a key role in ecosystem functioning (Lavelle 1996), has a cosmopolitan distribution (Anderson 1977) and its diversity encompasses many species with varied life-history traits in terms of diets, mobility and size (Usher et al. 1982; Koivula et al. 2002; Lindberg and Bengtsson 2006) allowing comparative studies in different environments and biomes. Soil and litter macrofauna has been used in various ecological studies for a long time (Roberts and Johnson 1978), especially in the context of a disturbance (Wanner and Dunger 2002; Comor et al. 2008), as they quickly respond to and re-establish after disturbances (Rosenberg et al. 1986).

Density – body mass relationship

To assess whether a community is impacted by a disturbance or has recovered, reliable indicators are necessary, reflecting the structure of a community and indicating whether it is balanced or not. In the case of disturbances, a relevant index should take into account species abundances and their life-history traits. Species abundance is an important ecological index that is impacted by disturbance (Armesto and Pickett 1985). Species are not all affected in the same manner by a disturbance (due to the ecological filter it creates), depending on their life-history traits (response traits; Prinzing et al. 2002; Comor et al. 2008) and they can play different roles in the recovery following a disturbance, some species facilitating the recovery because of their traits (function traits; Mendoza-Hernández et al. 2012). One trait in particular is a good indicator of the general traits of soil and litter macrofauna, as it encompasses many of the life-history traits of each species: body mass (Peters 1983; Peterson et al. 1998; Lewis et al. 2008). Therefore, I used the density – body mass relationship (DBM relationship), which is based on these two fundamental ecological indices, to test whether it could reflect changes in a community's structure and functioning after a disturbance, and in similar environments varying in productivity. Moreover, the shape of the DBM relationship is highly debated (Brown and Maurer 1987; Gaston and Lawton 1988; Nee et al. 1991; Leaper and Raffaelli 1999). I will investigate in this thesis whether this shape depends on disturbances and the following recovery (Chapter 4).

Outline of the thesis

In this thesis, I test the effect of productivity, different community compositions and varying environmental conditions on the structure of soil and litter fauna communities after a disturbance. I investigate the impact of these characteristics on the ensuing recovery and try to highlight the life-history traits playing a determining role for communities facing a disturbance.

In the second chapter of this thesis, I compare the impact of a similar disturbance in two climatically contrasting biomes, and the subsequent recovery, with the means of an index that I propose, to measure the impact of a disturbance and the recovery of litter fauna communities. I sampled litter macrofauna in a boreal and a temperate forest to study how it was impacted by a disturbance that I created. I hypothesize that the communities of the temperate forest would recover faster, due to the higher annual temperatures and to the higher species richness and abundance. I also predict that, within each biome, higher species richness would not benefit to the communities, as the disturbance used would equally affect all arthropods (irrespective of their life-history traits), and that communities with an initial higher species abundance would be less impacted, as their surviving fraction would be more important than the one of low-abundance communities.

In Chapter 3, I study species assembly of the same communities as in the previous chapter in order to estimate whether these assemblages could be explained rather by the niche or the neutral theory. I compare the similarity in space and time of the communities between and within the temperate and the boreal forests. My main hypothesis is that communities from the boreal forest would re-establish more similarly to their pre-disturbance composition and to the surrounding community composition, than temperate communities, because of the lower productivity and species richness and abundance of the boreal forest.

Chapter 4 focuses on the DBM relationship to test whether this relationship reflects and can help explaining different structures of communities after a disturbance. I use soil and litter macrofaunal communities from a semi-arid environment and a similar disturbance as in the previous chapters. I hypothesize that, just after the disturbance, the slope of the DBM relationship will increase if small animals are more impacted than large ones or decrease in the opposite situation. I also test that the DBM relationship can reflect whether a disturbed community is recovering.

Based on the knowledge acquired from Chapter 4, I use the same relationship in Chapter 5 and test its ability to reflect differences between soil and litter macrofaunal communities from tidal marshes subject to varying intensities of a stress (sea inundation frequency) in combination with a disturbance (cattle grazing). I hypothesize that the differences in productivity (due to sea inundation frequency) of the different areas in which the animals were collected will be reflected in the DBM relationships, with the prediction that the slope will increase if the larger animals benefit more than the smaller ones from higher productivity.

Finally, in the last chapter of this thesis, I present a synthesis based on the results of the previous chapters about the impact of the types of disturbance I use in this thesis, the influence of environmental factors and the effect of the composition of communities on the structure of soil and litter fauna communities.

CHAPTER 2

Resistance and recovery of soil fauna communities after a disturbance in two contrasting biomes

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ABSTRACT

The effects of anthropogenic disturbances on communities and the recovery of the latter are central topics in biodiversity conservation, but predictive theory about both the effects of environmental conditions on this recovery and the recovery itself is lacking. As mean annual temperatures are higher toward the equator, we consider energy as the main environmental difference between a boreal and a temperate forest, and we hypothesize that recovery would be faster in the low latitude biome. However, we hypothesize that energy would not affect the ability of either community to resist a similar disturbance. We test these hypotheses by comparing the effects of an identical disturbance (diesel fuel spraying) on litter macrofauna communities of a boreal and a temperate forest. The leaf litter layer protected the temperate communities and the impact of the disturbance was much greater in the boreal forest, where there was no litter layer. In the boreal forest, high abundance communities did not resist the disturbance better than low abundance ones. Good dispersers were able to flee from the disturbance and they were also the first colonisers. Local factors (litter layer, surrounding species pool) were more important for the resistance and recovery of communities than differences between the energy received by the biomes. Thus, predicting and explaining the consequences of a disturbance, and adapting conservation plans, will only be possible if the characteristics of the disturbance and of the environment, as well as the functional structure of the communities are known.

INTRODUCTION

Effects of disturbances on ecosystem functioning, such as habitat destruction, biomass removal or food web disruption, have long been studied (White 1979). Numerous studies have contributed to better understanding their consequences on biodiversity (Richmond 1993; Vörösmarty and Sahagian 2000; Benedetti-Cecchi et al. 2001; Gullison et al. 2007) and ecosystem stability (Hooper et al. 2005). However, the recovery processes following disturbances are still poorly understood (Brudvig 2011); for instance, it is not yet clear how functional traits are impacted by different anthropogenic environmental changes nor how they recover (Hooper et al. 2005). The re-establishment of communities can take place locally, by the population development of surviving species, or regionally, by recolonization of species from the surroundings, or both (Bengtsson 2002). Local factors, such as the rate of survival and the reproductive success (which depends on the disturbance's type and intensity, Sousa 1984), as well as regional factors, such as the pool of species around the disturbed areas and their dispersal capabilities, will determine which process is fundamental for the recovery.

Regarding ecosystem recovery, a species-rich community has both a higher functional diversity and redundancy of traits (different species carrying similar traits) (Naeem et al. 1999), and, consequently, would be more capable of resisting and recovering from a disturbance (Frank and McNaughton 1991; Tilman and Downing 1994), i.e., the "insurance hypothesis" (Naeem and Li 1997). Species abundance may also contribute to a community's resistance and recovery: if a disturbance randomly affects only a certain fraction of a community (all species being similarly affected), a high species abundance would be an advantage for a community's resistance and recovery, the post-disturbance abundance being higher if the community's pre-disturbance abundance was high.

Biomes near the (thermal) equator receive more energy (in the form of light and heat) than those situated at higher latitudes. This could have direct and indirect consequences for the recovery of ecosystems after a disturbance. Firstly, energy can enhance the recovery of ecosystems by accelerating physiological processes (Deangelis 1980; Brown et al. 2004) of the organisms pertaining to both the aforementioned local and regional re-establishments. This means that an ecosystem would recover more rapidly when located closer to the equator. Secondly, the primary productivity of ecosystems also depends on the amount of energy they receive (and on the availability of other resources, such as water and minerals), and productivity and species richness are usually thought to be positively correlated (i.e., species – energy relationship, Gaston and Blackburn 2000, Qian and Xiao 2012, but see Adler et al. 2011). As ecosystem productivity (i.e., resource availability) also regulates population density according to the energy–limitation hypothesis (Wright 1983; Kaspari et al. 2000), and as productivity is higher at lower latitudes, we can also assume species' total abundance to be higher at lower latitudes. Consequently, one could expect ecosystem recovery to be enhanced at lower latitudes.

Our main objective is to determine whether the recovery of forest litter communities following an equal disturbance in a temperate (representing a high-energy system) and a boreal biome (a low-energy system) differs in terms of speed (i.e., how fast they recover compared to one another) and trajectory (i.e., which life-history traits are involved). In these two biomes, we study the resistance and recovery of forest litter macrofauna communities impacted by a disturbance. We choose this group because of its key role in ecosystem functioning (Lavelle 1996), its quick response to disturbances and ability to re-establish (Rosenberg et al. 1986), as well as its broad variety of traits (Usher et al. 1982; Rosenberg et al. 1986; Koivula et al. 2002; Lindberg and Bengtsson 2006; Makkonen et al. 2011).

Firstly, preceding the recovery, we expect the resistance to the disturbance of both the boreal and temperate communities to be similar, as their richness may not differ (De Deyn and van der Putten 2005) and as we do not expect environmental conditions (i.e., forest structure and temperature during the growing season) to influence such a short-term event, despite the common idea that different environmental conditions can affect the impact of a disturbance (National Research Council 1981; Sousa 1984). Within the same biome, we expect communities exhibiting higher total abundance to better resist the disturbance, as the latter may eliminate a proportion of the total abundance of the community (therefore, the higher the initial abundance, the higher the remaining abundance after the disturbance). Likewise, within each biome, we expect high-species richness communities to have a higher resistance, thanks to their higher trait diversity (Naeem 1998; Yachi and Loreau 1999).

After the disturbance, we expect the different climatic conditions (mainly defined by the lower temperatures in the boreal forest) to have an effect on the recovery. We hypothesize that the litter macrofauna of the temperate forest will recover faster (in terms of abundance, richness and biomass) because of the higher annual temperatures and the shorter winter period. As the largest part of the litter macrofauna has a reproductive cycle of one year (Ribera et al. 1999; Turin 2000), we expect recolonization from the surroundings to be the main source for the re-establishment of the communities within the year following the disturbance, rather than from surviving animals.

In order to create a rapid and short-lasting impact on litter macrofauna, we use diesel fuel as a pulse disturbance, due to its toxicity to fauna (Shell UK Oil Products 2008). Moreover, the global use of petroleum-derived fuels makes them one of the main potential sources of environmental contamination (Rosenberg and Ron 1996; Iloba and Jarrett 2007). Hydrocarbons appear to impact different soil macrofauna species in the same way (trial experiment, data not shown), therefore the latter are equally susceptible to be affected. Diesel fuel impacts animals and plant communities rapidly but does not destroy community habitat when sprayed in relatively low amounts, allowing litter fauna to recover within a few months (Jones and Schmitz 2009).

METHODS

Study sites

Fieldwork for the temperate deciduous forest took place in Klarenbeek, the Netherlands (52°10'49"N, 6°6'21"E), in a forest dominated by oak (Quercus robur). The forest floor was covered with a thick leaf litter layer (5 to 10 cm). The boreal forest, situated in Rusutjärvi, Finland (60°27'2"N, 24°57'23"E), consisted of a mixed forest of spruce (Picea abies), birch (Betula pendula) and red pine (Pinus resinosa). The forest floor was mainly covered with varying densities of grass, moss, ferns and cranberry shrubs. The climate of the two sites during the annual period of Sampling Is presented in Table 1. The average temperature during the time of the experiment was almost twice as high in the boreal forest (10.2°C vs. 5.9°C), but extreme temperatures were rather close in both sites. Precipitations were 25% more important in the temperate forest than in the boreal one. The forest floor of the boreal forest was covered with snow from late November till early April.

Table 1: Climate of the two study sites during the experiment (Dutch data: Ministerie van Infrastructuur en Milieu (2011); Finnish data: courtesy of METLA).

	Minimum temperature	Maximum temperature	Average temperature	Annual precipitations
Temperate	-18.4°C	35°C	10.2°C	827 mm
Boreal	-24.8°C	32.5°C	5.9°C	658 mm

Experimental design

Sampling occurred following a randomized block design consisting of five blocks (i.e., replicates) of three treatment plots of 100 m2 (circles of 5.6 m in radius): a “control”, a “light disturbance” and an “intense disturbance” plot. Plots were separated by 20 m and blocks were separated by at least 100 m. In each plot, 12 pitfall traps were placed according to two sampling rings: an inner one, 2 m from the centre, and an outer one, 4 m from the centre (the six pitfall traps of each ring were evenly distributed along the circle they formed). The aim of this setup was to see whether the recovery would be due to animals recolonizing from the surrounding area (in which case the average abundance of macrofauna in the outer ring samples would be higher than in the inner ring’s) or due to offspring of survivors (then, the average abundance of macrofauna in samples of the inner and outer rings would be similar) (cf. Antunes et al. 2009). The disturbance was created by spraying the same brand and quality of diesel fuel (i.e., Shell regular diesel fuel) on the forest floor of the two sites with a backpack sprayer; 50 ml.m^{-2} for the light disturbance and 250 ml.m^{-2} for the intense one (nothing was sprayed on the control). A trial experiment had been carried out by spraying various doses of diesel fuel on the litter layer of the temperate forest in April 2009: 50 ml.m^{-2}, 100 ml.m^{-2}, 250 ml.m^{-2}, 500 ml.m^{-2}, 1000 ml.m^{-2}; the smallest dose proved to be sufficient to significantly impact the macrofauna (50% decrease of the total abundance) and

250 ml.m^{-2} decreased the total abundance to roughly 10% of the original one (results not shown).

Sampling of soil fauna

Sampling occurred four times in both biomes: three weeks before the disturbance (i.e., the reference, thereafter named Sampling I), giving enough time for the animals to recolonize before the disturbance, and then, one day, four months, and one year after the disturbance (respectively thereafter referred to as Sampling II, III and IV). The first sampling occurred in May 2009 in the temperate forest and in June 2009 in the boreal forest. Soil macroarthropods were collected by means of 10 cm wide and 12 cm deep pitfall traps containing 2 cm of salt-saturated water as a preservative. A 20 × 20 cm white plastic roof was placed 5 cm above the traps to protect them from the rain and direct sun light. During each sampling, pitfall traps were open for 10 days and each plot was surrounded by a 30 cm high plastic enclosure, of which 5 cm were buried. This prevented animals from entering or leaving the plots during sampling, in order to obtain a better estimate of the total abundance within each plot (Desender and Maelfait 1986). When the disturbance was applied, the pitfall traps were closed and there was no enclosure around the plots. At the end of each sampling session, pitfall samples were sieved into a strainer and rinsed to eliminate the salted water that was replaced by 70% ethanol for long-term preservation.

Identification was undertaken with a stereoscopic microscope to the species or the family level. Morphospecies were sometimes used within some families, based on the size (small, medium, large) of the animals (see Table 1 of Appendix 1 for details). Owing to their scarcity and to taxonomic difficulties, larvae, nymphs and pupae were not taken into account. For some samples where ants were very numerous, an estimate of the total number of individuals was undertaken by counting the animals in a quarter of a Petri dish.

Traits

Life-history traits of species were diet, body weight and dispersal capabilities. Diet were attributed to the different species according to Hatteland & Hauge (2007), Ribera et al. (1999), Turin (2000), Loubère (2011) and to Wim Dimmers and Theodoor Heijerman (pers. comm.). Each species was categorised in one or more of the following feeding groups: omnivorous, carnivorous, phytophagous, coprophagous, necrophagous, saprophagous and fungivorous. Dry body mass was determined by weighing ten randomly selected individuals of each species (when possible, otherwise, all of the available individuals of the species) after they had been dried at 60°C for 48 hours (following Rogers et al. 1977). Total dry biomass was calculated using the species' mean dry body mass multiplied by their respective abundance in each sample. Dispersal capability was rated on a scale from 1 (low dispersal capability) to 5 (high dispersal capability) according to literature, based on flight ability and body size (Turin 2000, Hatteland and Hauge 2007, Jenkins et al. 2007, Wim Dimmers and Theodoor Heijerman pers. comm).

Recovery index

As a community can recover and yet have a different structure (in terms of species richness, abundance, biomass and trait abundance) than its pre-disturbed state, due to natural and seasonal variations, we created an index to determine the recovery of a community that accounted for these natural variations. We computed a recovery index (RI) for the three sampling sessions following the disturbance, for each of the following ecological indices: species abundance, species richness, biomass, and abundance of single life-history traits. The RI was then ln-transformed as follows:

$$RI = \ln\left(\frac{\frac{D_{1+t}}{D_1}}{\frac{C_{1+t}}{C_1}}\right) = \ln\left(\frac{C_1 \times D_{1+t}}{C_{1+t} \times D_1}\right)$$

Where $\frac{D_{1+t}}{D_1}$ is the change in the disturbed plots and $\frac{C_{1+t}}{C_1}$ the change due to natural and seasonal variations, with

- D_1 as one of the above-mentioned ecological indices of the considered sample in the disturbed plot at Sampling I (the reference: t = 0)
- D_{1+t} as the ecological index of the considered sample in the disturbed plot at Sampling II, III or IV (t = 1, 2 or 3)
- C_1 as the ecological index of the considered sample in the control plot at Sampling I (the reference: t = 0)
- C_{1+t} as the ecological index of the considered sample in the control plot at Sampling II, III or IV (t = 1, 2 or 3)

If $\frac{D_{1+t}}{D_1}$ was greater than $\frac{C_{1+t}}{C_1}$, then the variation of the considered ecological index was due to the disturbance rather than to natural and seasonal variations. If the RI was positive, this meant that the considered ecological index had increased compared to both the reference and the natural variation. Conversely, if the RI was negative, the ecological index had then decreased compared to the reference and to the natural variations, meaning that it was not as high as during the first sampling and so, indicating an incomplete recovery of this ecological index. The mean of the RIs of all the samples of the five replicates (either lightly or intensely disturbed) was calculated.

Effects of the disturbance on soil properties

As it was not possible to directly measure the quantity of diesel fuel that percolated into the ground, we measured other ecologically relevant abiotic soil factors, such as the pH and the percentage of soil organic matter, carbon, nitrogen and phosphorus. We collected some litter of the first five centimetres of the forest floor (ca 50 g of dead leaves and top humus per plot) in each of the plots during the four sampling sessions, dried it at 50°C for 48 hours and preserved it in sealed bags.

Before the disturbance, the forest soil of both biomes had similar soil organic matter content (92% w/w in the temperate forest and 93% w/w in the boreal forest), carbon content (47% w/w in both forests), nitrogen content (2% w/w in both forests), phosphorus content (0.1% w/w in both forests) and pH (4.6 in both forests, measured from the dried litter). No differences between the treatments were detected at any time in the temperate forest for all of the chemical analyses. In the boreal forest, only the percentage of carbon increased significantly at Sampling II in the disturbed plots (Repeated Measures ANOVA, Treatment: $F_{2,12} = 4.8$, $P = 0.029$, Time: $F_{2.1,\ 25.1} = 16.4$, $P < 0.001$; Time x Treatment: $F_{4.2,\ 25.1} = 5.3$, $P = 0.003$) from an average of 47.5% in the control plots to 49.4% in the lightly disturbed ones and 51.8% in the intensely disturbed ones (the percentage of carbon in the disturbed plots at the reference was equal to the control plots'). For the other sampling sessions in the boreal forest, there was no difference between the treatments and between the sampling sessions.

Statistics

Species – effort curves of each biome were computed with EstimateS (Colwell et al. 2004) based on the 180 samples (per biome) of Sampling I. Independent-samples t-tests were performed in SPSS to test for the differences in species abundance and richness between the inner and the outer sampling rings in both biomes. No difference was found between the inner sampling ring and the outer one, at any time, for the disturbed plots, for the species richness, species abundance and total biomass, for both biomes (see Table 2 of Appendix 1); the data of the 12 samples of each plot were therefore pooled for further analyses, when required.

To test whether the RIs for species abundance, richness and biomass were different from zero, one-sample t-tests were performed. Univariate GLMs were performed on the RIs based on life-history traits to determine differences between the traits. The RI was set as the dependant variable, the considered trait (diet or dispersal capability) as a fixed factor, block as a random factor and the natural logarithm of the body mass was used as a covariate.

RESULTS

During the four sampling sessions in the two biomes, a total of 1 440 samples were collected, consisting of 191 900 individuals (38 511 in the Netherlands and 153 389 in Finland) distributed among 14 families. Within these families, 64 species, nine mophospecies and two families were used in the analyses (see Table 1 of Appendix 1). Total species richness in the temperate forest (55 species) was similar to the one in the boreal forest (53 species) (independent-sample t-test on the cumulated richness of

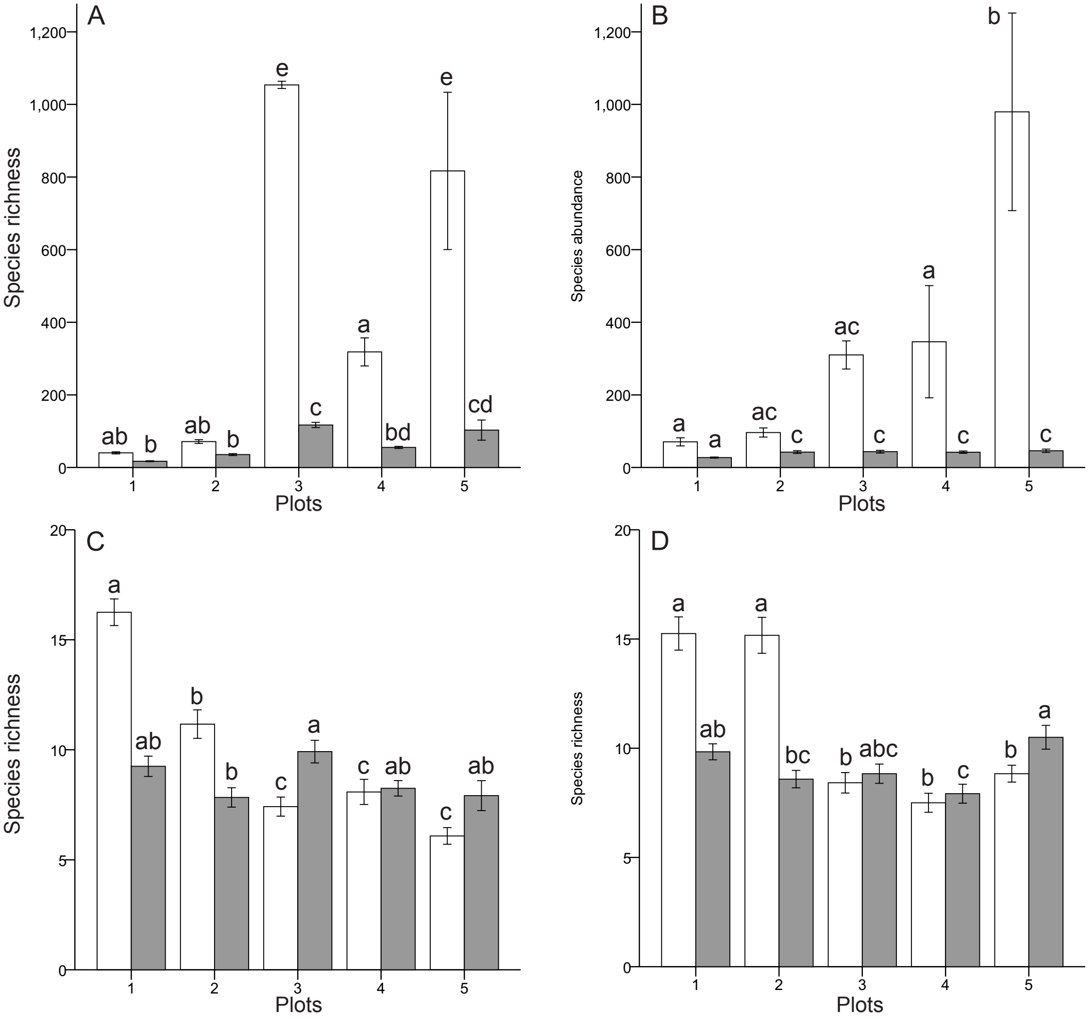

Figure 1: Estimated marginal means of total community abundance per sample (±1SE) of the five (A) lightly and (B) intensely disturbed plots (replicates), and of total species richness per sample in the five (C) lightly and (D) intensely disturbed plots, at sampling I (white) and II (grey) in the boreal forest. Letters indicate significant differences between either treatments or sampling sessions.

both biomes in all plots and at all samplings: $t_{(38)} = 1.643$, $P = 0.109$). Species – effort curves indicated that with increasing the number of samples further, we would not have found many more species (see figure 1 of Appendix 1).

Resistance of communities

The disturbance did not seem to have any impact in the temperate forest. In the boreal forest, the five lightly disturbed and the five intensely disturbed plots exhibited a broad range of species abundance and richness at Sampling I, so we could test whether these ecological indices contributed to the resistance of a community facing a disturbance. The abundance at the reference (Sampling I) did not seem to influence the subsequent

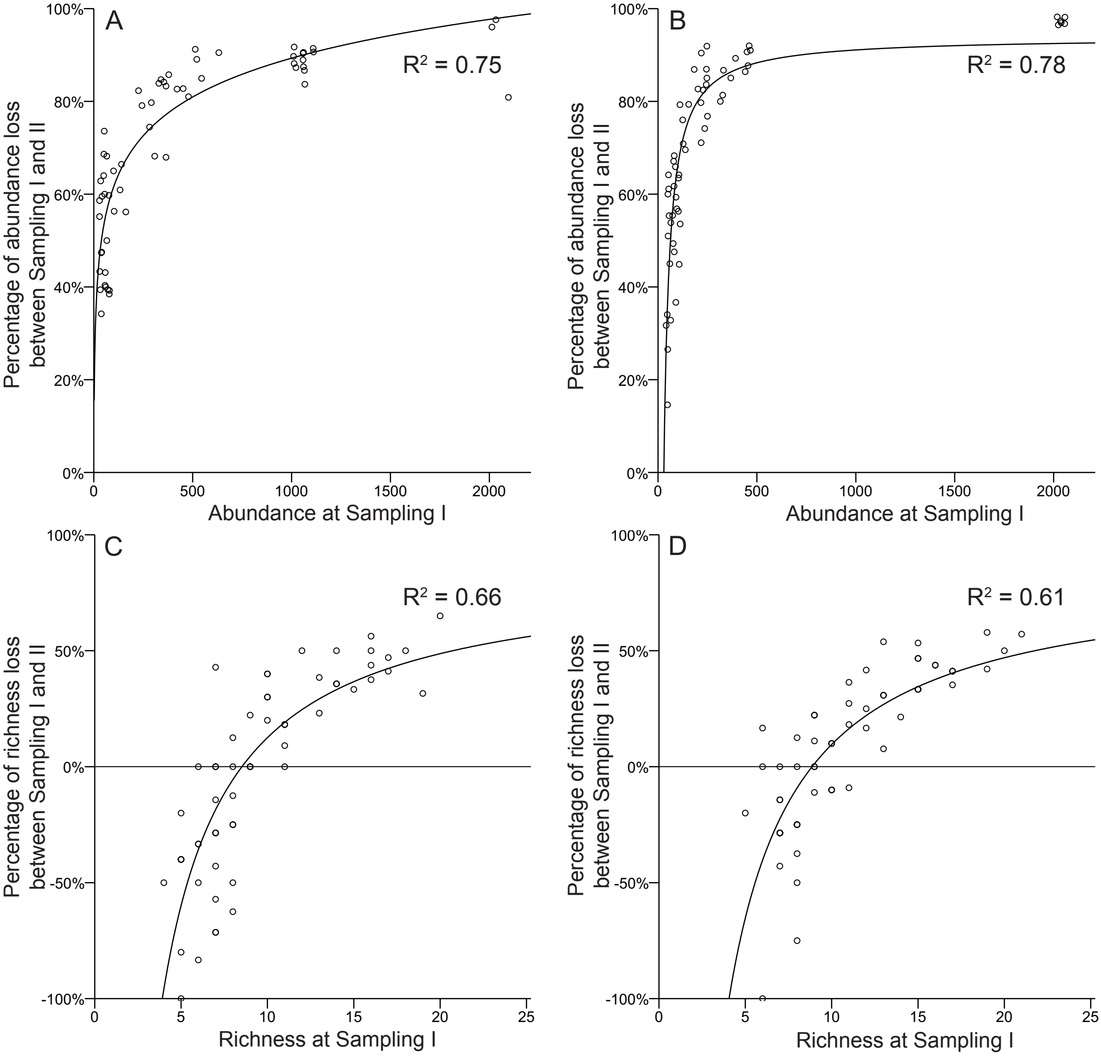

Figure 2: Percentage of community abundance loss per sample between Sampling I and II versus community abundance per sample at Sampling I in the boreal forest (A) for the lightly disturbed communities (best fit with a log function) and (B) for the intensely disturbed communities (best fit with an inverse function). Idem for the species richness (C) for the lightly disturbed communities (best fit with an inverse function) and (D) for the intensely disturbed communities (best fit with an inverse function).

abundance just after the disturbance (Sampling II): the five lightly disturbed plots showed some differences between their post-disturbance abundances at Sampling II (Figure 1.A), but the intensely disturbed ones had almost the same subsequent abundance at Sampling II, regardless of their abundance at the reference (Figure 1.B).

By plotting the proportional loss of community abundance between Sampling I and II against the species abundance per sample at Sampling I, we obtained the best fit with a logarithmic relationship in the case of the lightly disturbed communities (Figure 2.A) and an inverse relationship with the intensely disturbed communities

(Figure 2.B). Species richness showed a different pattern (Figure 1.C and 1.D): the samples that had a low species richness at the reference were likely to see their richness increase after the disturbance (expressed by a negative percentage of loss, Figure 2.C and 2.D), especially the lightly disturbed ones. A higher richness at the reference appears to prevent from a drop of a community's richness only to a certain extent: according to the trend line, the richness should be higher than 20 species for at least half of the species to survive.

Species abundance, richness and biomass

In the temperate forest, the RI for abundance of both the lightly and intensely disturbed plots was positive at Samplings II, III and IV (Figure 3.A), showing that the abundance in the disturbed plots increased significantly more than in the control plots (results of the t-tests are shown in Table 3 of Appendix 1). However, in the boreal forest, the index was negative at Sampling II (Figure 3.B): in this biome, the abundance decreased directly after the disturbance. The RI for richness showed a highly significant increase in the temperate biome just after the disturbance for both the lightly and intensely disturbed plots (Figure 3.C), whereas no significant change occurred in the boreal forest (Figure 3.D). Biomass increased in the lightly disturbed communities of the temperate forest, but not in the intensely disturbed ones (Figure 3.E). In the boreal forest, following the trend of the abundance, the biomass significantly decreased just after the disturbance, for both disturbance intensities (Figure 3.F).

At Sampling III, the RI for abundance was positive in both biomes (Figure 3.A and 3.B); the RI for richness did not differ from zero, except for the lightly disturbed plots of the boreal biome where it was positive (Figure 3.C and 3.D). The RI for biomass did not differ from zero in the temperate forest (Figure 3.E), but was significantly positive in the boreal forest (Figure 3.F).

With the exception of the richness of the lightly disturbed communities in the boreal biome, all the RIs at Sampling IV were not significantly different from zero. Overall, there was no difference between the light and intense disturbance treatments.

Community diet profiles

In the temperate forest, before the disturbance, the community was largely dominated by saprophagous and omnivorous species, which represented more than 80% of the total community abundance (Figure 4.A, 4.B and 4.C). The disturbance seems to have decreased the relative abundance of saprophages and increased the proportion of omnivores. Carnivores, necrophages and coprophages were relatively more abundant at Sampling III in all treatments. One year after the disturbance, the relative abundance of the saprophages increased in all treatments and represented more than 70% of the community, at the expense of the other feeding groups.

The boreal community was largely dominated by omnivorous species before the disturbance (around 95%), followed by the saprophages (less than 4%) and the carnivores

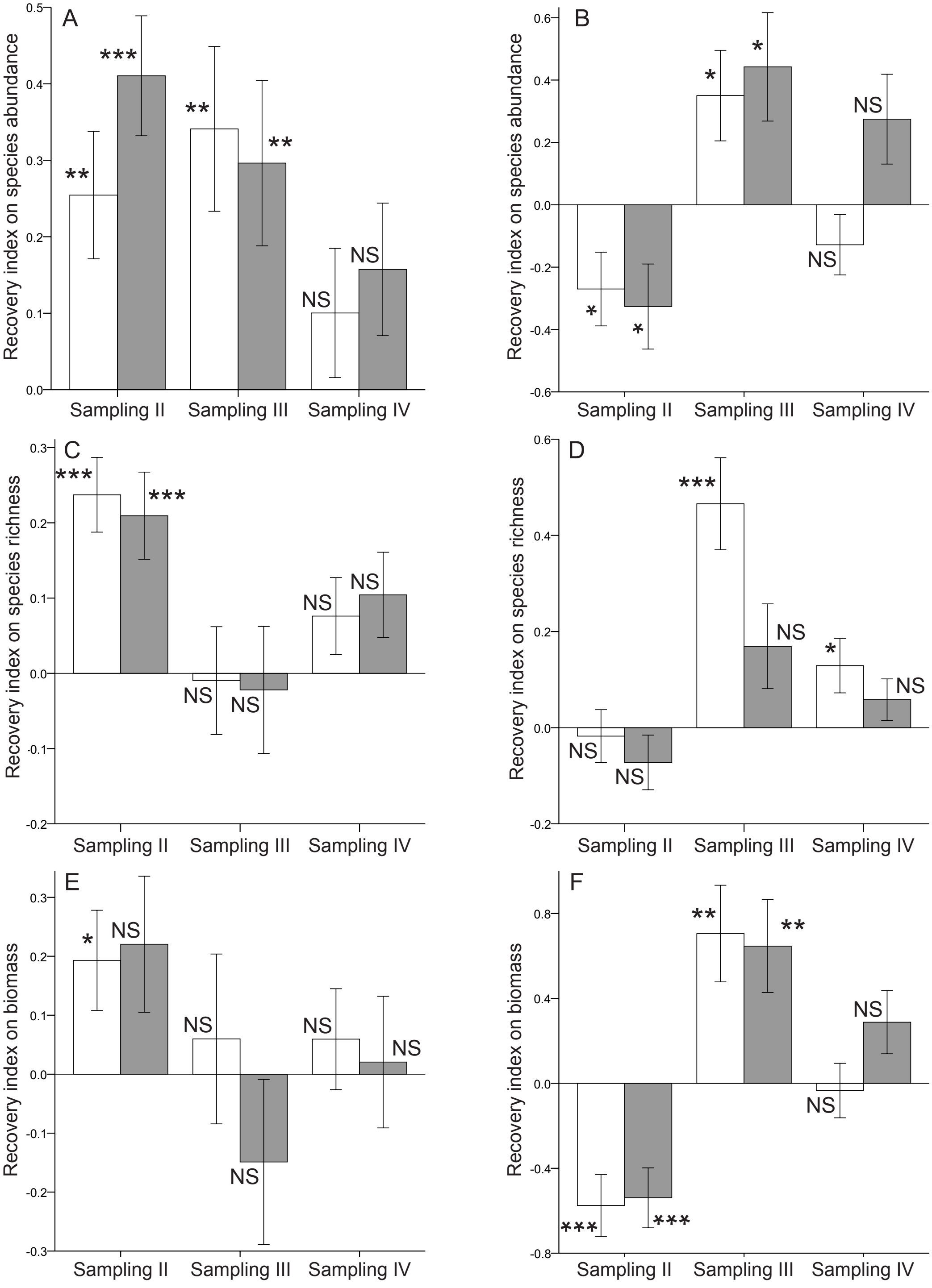

Figure 3: Mean recovery index (±1SE) at Sampling II, III and IV for species abundance (A) in the temperate forest and (B) in the boreal forest, for species richness (C) in the temperate forest and (D) in the boreal forest, and for species biomass (E) in the temperate forest and (F) in the boreal forest. White bars: light disturbance; grey bars: intense disturbance. One sample t-tests: NS: Not Significant, *: $P \leq 0.05$, **: $P \leq 0.01$, ***: $P \leq 0.001$.

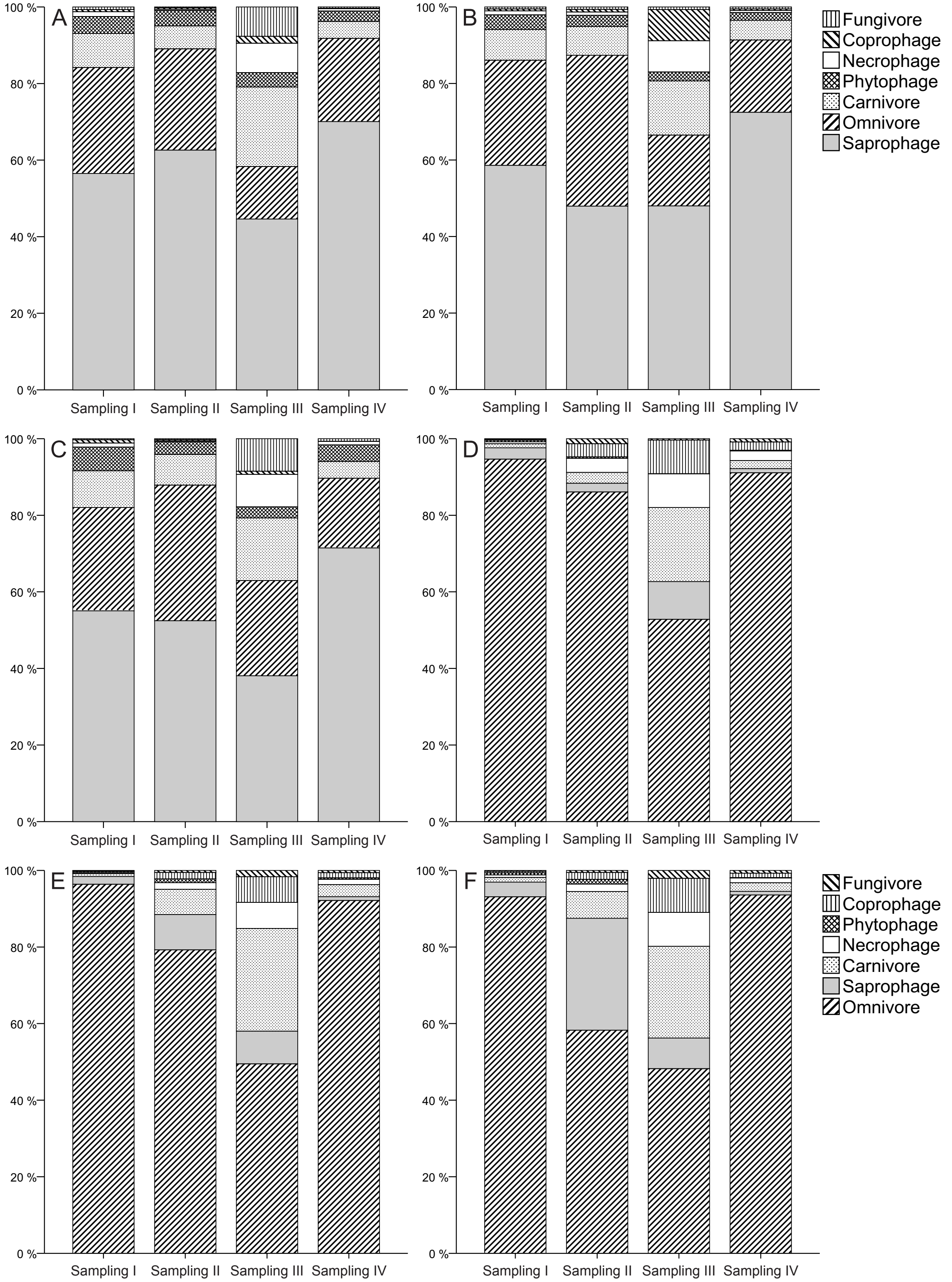

Figure 4: Relative abundances of the diets at the four sampling times in the temperate forest (A) for the control plots, (B) the lightly disturbed plots and (C) the intensely disturbed plots, and in the boreal forest (D) for the control plots, (E) the lightly disturbed plots and (F) the intensely disturbed plots.

(1%) (Figure 4.D, 4.E and 4.F). All three treatments exhibited very similar community structures at all samplings, except for Sampling II, where there was a small disruption in the lightly disturbed communities and a major one in the intensely disturbed ones. The disturbance seems to have severely decreased the relative abundance of the omnivores to the benefit of saprophages and carnivores. At Sampling III, carnivores represented more than 20% of the community, and necrophages and coprophages seemed to be more numerous than previously; this increase could also be observed for the two other treatments. Finally, at Sampling IV, the structure of the disturbed communities resembled the reference's one and was, as well, similar to the one of the last sampling session of the control communities.

Community trait compositions

The analyses of the recovery indices for the life-history traits showed that, just after the disturbance, in the lightly disturbed plots of the temperate forest, the smaller arthropods were more numerous compared to the control plots (GLM $F_{1,67} = 5.529$, $P = 0.022$). Confirming this, the dispersal capabilities (which are related to body mass) of the arthropods in the boreal forest showed a significant negative response to the intense disturbance ($F_{4,20.522} = 7.825$, $P = 0.001$): the slowest animals appeared to still be present while the good dispersers were significantly less numerous (Figure 5.A). At Sampling III, these differences disappeared ($F_{4,17.497} = 2.287$, $P = 0.101$; Figure 5.B).

No feeding group in particular showed any increase or decrease of its RI just after the disturbance in the temperate forest, where the total abundance increased. At the same time, in the boreal forest, some feeding groups have seen their RI decreasing significantly lower than the rest of the community, such as the necrophages ($F_{1,4.264} = 9.783$, $P = 0.032$) and the fungivores ($F_{1,15.957} = 5.111$, $P = 0.038$). One feeding group showed

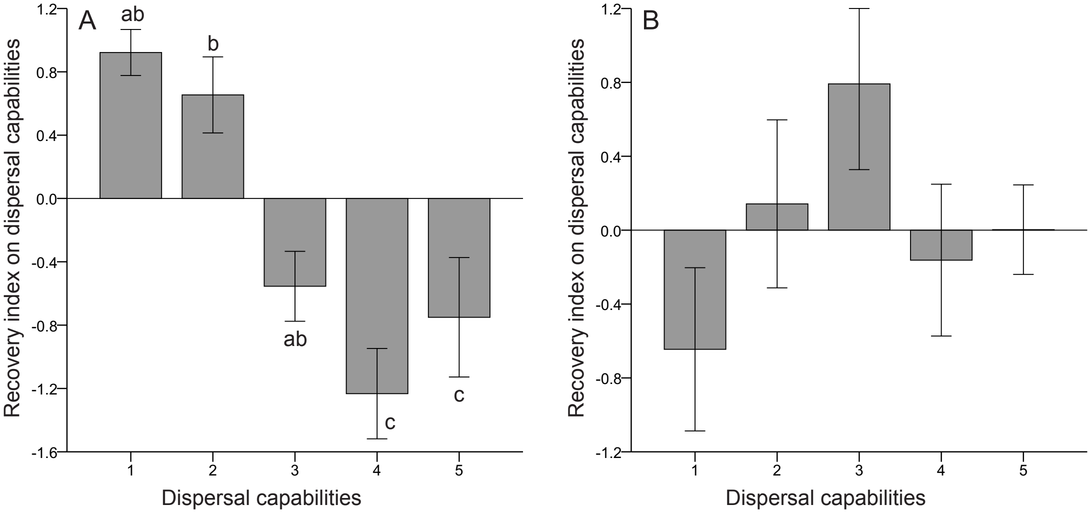

Figure 5: Mean recovery index (±1SE) for the five categories of dispersal capabilities (A) at Sampling II and (B) at Sampling III of the intense disturbance plots in the boreal forest. Letters indicate significant differences between dispersal categories.

an opposite trend to the previous ones: the saprophages' relative abundance increased at Sampling II ($F_{1,5.483} = 25.780$, $P = 0.003$). The RI for the body mass at Sampling IV in the boreal forest showed a significantly higher proportion of bigger animals both in the lightly ($F_{1,58} = 5.682$, $P = 0.020$) and the intensely ($F_{1,67} = 7.027$, $P = 0.010$) disturbed plots, and so did the RI for carnivorous animals (usually bigger) in the lightly disturbed plots ($F_{1,9.513} = 5.585$, $P = 0.041$).

Discussion

Recent emphasis in ecology on the relationship between biodiversity and ecosystem functioning has highlighted how disturbances affect stability over time (Loreau et al. 2001; Jiang and Pu 2009). Stability is here used as a measure for the probability of an ecosystem returning quickly to a previous state, but a wide array of different properties contributes to it (Pimm 1984). In this study, we analyse two properties of stability, namely resistance and recovery (we will not talk about resilience, as it is a return time to equilibrium of a system, which we did not measure).

Regarding the resistance of communities in the boreal forest, we find no effect of a community's total abundance on resistance to the applied disturbance (Figure 1.A and 1.B) as both high- and low-abundance communities exhibited a very similar abundance after the disturbance. In fact, high abundance communities were proportionally more impacted than the ones with a previously lower abundance (Figure 2.A and 2.B). It seems that the percentage of species richness loss levels off at about 50% (Figure 2.A and 2.B), meaning that it is beneficial for a community to exhibit a high richness, as half of its species is still preserved after a disturbance such as the one we used, increasing the chance of recovery and supporting the insurance hypothesis (Naeem & Li 1997; Yachi & Loreau 1999). Moreover, contrary to the abundance, the average species richness in the boreal forest did not significantly decrease. Therefore, it appears more important for a community's resistance to have a high richness rather than a high total abundance. It has previously been shown that a broad spectrum of life-history traits within a functional group also increases its resistance (Schweiger et al. 2007). The diversity of traits within a functional group promotes recovery and, thus, could be considered for further studies.

Because the disturbance has a measurable impact only in the boreal forest, we cannot show whether or not resistance can be directly facilitated by a more productive environment. This surprising resistance of the macrofauna communities in the temperate forest is even followed by an increase in species richness and abundance just after the disturbance (Figure 3.A and 1.C). Two explanations could help understanding these unexpected findings: first, a protective effect and then, an attractive effect. We suggest that the thick leaf litter layer that covered the temperate forest floor played an important protective role for the animals that were already present. The diesel fuel sprayed on the surface might not have reached the macrofauna, which found refuge underneath. Confirming this assumption, in the boreal forest, where there was almost no litter layer on the forest floor, the total species abundance decreased just after the disturbance (Figure 3.B). The litter layer is known for protecting the soil's structural integrity (i.e., the soil's pores) upon which the fauna depends (Bridge et al. 1983), for providing a shelter to the fauna by regulating the temperature and moisture (Gill 1969; David et al. 1991) and, it was shown to protect caterpillars, which could hide from predating ants (Karban et al. 2013). Our results suggest that the litter layer can greatly contribute to the resistance of a whole community seeking refuge into it and this environmental element should not be neglected in future cases involving a disturbance in a litter-covered area. The absence of impact of the disturbance is thus not directly due to the temperate biome's milder climate, but to the presence of a structural environmental element. Regarding the increase in species richness and abundance, we speculate that the diesel fuel attracted some arthropods. For instance, directly after the disturbance (Sampling II), we collected tens to hundreds of Staphylinidae per sample of the disturbed plots, which were absent at Sampling I; their abundance increased with the dose of diesel fuel (these very species have not been considered for the analyses). The only explanation for this attractive effect is that some arthropods confused the odour of diesel fuel with decaying wood (T. Heijerman & O. Vorst, pers. comm.), but nothing in the available literature can support this statement.

At the scale of each biome, the mean species richness does not differ between the two biomes at the reference, confirming De Deyn and van der Putten's findings (2005), and it does not decrease just after the disturbance in either biome (Figure 3.C and 3.D). The disturbance may have reduced the populations of the different species (in the boreal forest), but did not eliminate any species when considering all the samples of each biome. Results of studies that focused on richness after a disturbance are contradictory, some finding a decrease (Vieira et al. (2004) in fresh water communities), others an increase (Nkwabi et al. (2011) in a savanna). A decrease in species richness can be explained by a selection by a disturbance that sometimes leads to the complete disappearance of species that cannot avoid or cope with a disturbance (Comor et al. 2008), whereas an increase may be due to newly available resources for new species (Collins et al. 1995; Huxham et al. 2000). According to the "More Individual Hypothesis" (Wright et al. 1993), a resource addition increases the abundance and the richness of a system, and a disturbance decreases the richness by reducing the number of individuals (McGlynn et al. 2010). Our results do not support this theoretical decrease in richness, which might be because it is very hard to remove all individuals of a large population and, paradoxically, at the same time, the few animals of a small population (in both cases, the last ones are hard to reach by the disturbance).

The disturbance had a strong effect on some particular species, depending on their life-history traits. The relative abundance of small species and bad dispersers increased just after the disturbance (Figure 5.A), comparatively to the big species and good dispersers, suggesting that, in both biomes, the good dispersers were able to flee from the disturbance (dispersal capabilities are usually related to body mass (Brown et al. 2004; Jenkins et al. 2007)). This could also mean, on the contrary, that the good dispersers had quickly died because of the disturbance (before they fell in the pitfall traps at Sampling II), but the field observations (i.e., running and flying insects as we were spraying the diesel fuel) support the first hypothesis.

Both biomes had already recovered at Sampling III, according to the recovery indices for abundance, richness and biomass (Figure 3). This result is in agreement with Jones & Schmitz (2009), who showed that ecosystems can recover rapidly (especially after an oil spill), and with Antunes et al. (2009), who had also observed a fast recovery of litter macrofauna after an even more severe disturbance (i.e., a fire, which also modified the habitat). Contrary to our hypothesis, the climatic conditions of the boreal biome did not impede the recovery relative to the temperate forest. This could be explained by a rapid degradation of diesel fuel and the favourable temperatures of the growing season, this short period of time then being sufficient for the recovery. Besides, from the high abundances of macrofauna collected in most of the plots during the reference sampling, we can infer that the abundance was high as well in the surroundings. This important macrofauna pool around the disturbed areas must have contributed to the rapid recolonization, thus enhancing the recovery (Holling 1973; Brudvig 2011).

One year after the disturbance, in the boreal forest, the top predators (carnivores) and larger animals were in high abundance, and the functional structure of the community had fully recovered, as also confirmed by the diet profiles at Sampling IV, which were similar to those of the reference (Figure 4). In both biomes, no feeding group was absent from the disturbed plots at any time, therefore the functional structure of both biomes was not completely altered.

As restoration ecology needs predictive capability (Cairns 1990), we address the feasibility of predicting the trajectory and rate of recovery of litter fauna communities based on the comparison of two climatically contrasting biomes. To date, the various mechanisms involved in the resistance and recovery of communities following a disturbance make it very hard to make good predictions on, for instance, which species will come back first and when the recovery will be completed (Brudvig 2011). Our study shows that the resistance and recovery of two communities can greatly differ, even if they exhibit a similar species richness. Contrary to our hypothesis, the contrasting climates do not directly play a role in the differences in resistance and recovery of both biomes. The difference in resistance is due to the leaf litter layer only present on the floor of the temperate forest. This could give some insight on the diversity – stability relationship (McCann 2000) and the importance of abiotic factors, which can have a major role in stabilizing a community. The recovery, however, is faster than we expected in the boreal forest and the duration of the growing season, with its mild weather, must be long enough for the re-establishment of the communities. We also show that a community's species richness may be less affected by a disturbance than species abundance. Our results on resistance and recovery suggest that resistance would rather be a local process, depending on the community's features (such as species richness) and the local characteristics of the environment (here, the leaf litter layer), and that recovery would mainly depend on regional factors, such as the surrounding species pool. This study also provides more information about the functions involved in the recovery; we can speculate that a disturbance similar to the one that we used (e.g., fire or short-term pollution) would first negatively affect small species and those that cannot escape from it (i.e., body mass could be a relevant predicting factor), but would be followed by a rapid recovery, highlighting the importance of dispersal capability as a main functional trait for a quick recovery. Consequently, we need to know the type of disturbance, the environmental conditions, as well as the functional structure of a community (Gondard et al. 2003) in order to make predictions about the stability of a community.

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CHAPTER 3

Similarity in soil fauna communities after a disturbance in two climatically contrasting environments: testing predictions from the niche and neutral theory

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Abstract

We considered the two main and opposite theories that try to explain species assembly (i.e., the niche and neutral theory) as not mutually exclusive and, instead of testing them directly, we tested their respective predictions and expected species assembly to be rather driven by deterministic factors in more constraining environments and rather stochastically-driven otherwise. We compared the similarity between replicates of litter fauna assemblages before and after a similar disturbance that we created in two climatically contrasted biomes: a boreal and a temperate forest. We hypothesized that recovered species assemblages would be more similar to one another in the boreal forest (most constraining biome) than in the temperate forest, due to a more deterministically-driven species assembly, whereas in the temperate forest, the milder environmental conditions would allow for more stochastic processes and thus, less similarity between species assemblages. We used the Bray-Curtis dissimilarity index on species and diet abundances, but previously, we simulated the results obtained with and without a Wisconsin double standardization and rejected this option. Surprisingly, we found more between-replicates variation in the temperate forest before the disturbance, but we also found that, when considering the species assemblage of each replicate before and after the disturbance, the similarity was higher in the boreal forest. Therefore, species assembly in constraining environments may be more influenced by deterministic factors and the predictability of recovering assemblages would be higher in these conditions than in a less constraining ones. Our results help understanding the role of environmental conditions in the context of recovery and contribute to more successful restoration of disturbed communities by pointing at the variable predictability of recovery depending on environmental constraints.

INTRODUCTION

The assembly of species communities has long been discussed (MacArthur and Wilson 1967; Simberloff and Wilson 1969) and different theories to explain assembly have been proposed (Connor and Simberloff 1979; Hubbell 2001; Chisholm and Pacala 2011; Haegeman and Etienne 2011). Two main positions oppose each other. On the one hand, based on the niche theory (Hutchinson 1957; Chase and Leibold 2003), species assembly is thought to be driven by deterministic factors, such as environmental conditions and species interactions, giving an important weight to species life-history traits. On the other hand, species assembly is hypothesized to be stochastically driven by processes such as random colonization, birth and death (Connor and Simberloff 1979). This (at least partially) stochastic assembly is at the core of Hubbell's neutral theory (2001). The neutral theory is commonly perceived as a null alternative to niche theory (Harte 2012). Recent studies have shown that these two positions are not mutually exclusive and that species assembly is rather explained by a combination of both (e.g., Adler et al. 2007; Chase 2007; Chase et al. 2009; Barber and Marquis 2011; Haegeman and Loreau 2011). As the composition of communities at a certain location (α-diversity) depends on the larger species pool at regional scale (γ-diversity), one of the predictions of stochastic assembly is that local communities may differ from one another (β-diversity or compositional variation across local sites), even when environmental conditions at these locations are similar. On the contrary, similar communities are predicted by deterministic assembly at the local scale when environmental conditions at these locations are similar, due to environmental conditions filtering similar species from the regional species pool based on their life-history traits (Chase 2010).

The regional species pool might differ along environmental gradients. For instance, at a global scale of terrestrial systems, species richness and species abundance increase toward the tropics (Hillebrand 2004). At lower latitudes, the regional species pool might thus be larger than at higher latitudes. Consequently, if species assembly is mainly stochastically driven, one can expect local species assemblages to be less similar at lower latitudes than at higher latitudes, due to the higher number of species combinations possible at lower latitudes, whereas the smaller species pool may limit random species assembly at higher latitudes. Moreover, the relative importance of stochastic processes is expected to depend on the harshness of the ecological filter, so that local species assemblages are more similar in harsh environments such as lower-productivity environments (Chase 2007, 2010). Chase (2010) found higher β-diversity at higher productivity that resulted from a stronger role of stochastic relative to deterministic assembly processes with increasing productivity. Given that the harshness of the environment increases with higher latitudes (Billings 1987), this would support the expectation that communities would be more similar at higher latitudes.

It is thought that climate and energy play an important (but not exclusive) role in the biodiversity latitudinal gradient of terrestrial systems (Hawkins et al. 2003; Cardillo et al. 2005). Because energy and biodiversity are correlated along the latitudinal gradient, it is not clear which one is the main driving factor for the assembly of species communities. To test for the effect of energy on species assembly, we compared soil fauna communities in two climatically contrasting environments whose regional species pool sizes are equivalent (with temperature as a proxy for energy, provided that food resources are in sufficient amounts). In these sites, we studied soil fauna, since their latitudinal gradient does not follow the energy gradient and their richness and abundance do not increase toward the equator (De Deyn and van der Putten 2005; Comor et al. Chapter 2). These animals are particularly active in temperate and boreal forests, making these two biomes ideal locations for our study.

Species assembly can best be studied after a disturbance, when available resources allow for colonisation, and differences can be expected in the re-establishment of a community depending on its environmental conditions (Chase 2007). Soil fauna communities quickly respond to disturbances, re-establish rapidly after (Antunes et al. 2009; Comor et al. Chapter 2) and cover a large spectrum of functional traits (Usher et al. 1982; Rosenberg et al. 1986). In order to determine how communities establish in different environmental conditions, we studied the recovery of soil fauna communities after a light or intense disturbance in these two climatically contrasting biomes and compared the species and diet similarity of these communities within each biome.

Firstly, we investigated the initial dissimilarity between all of the communities (i.e., replicates) within each biome (β-diversity): we hypothesized that, before the disturbance, the similarity between the replicates in the temperate forest would be lower than in the boreal forest, due to the less constraining environmental conditions (Hypothesis 1) (Chase 2010).

Directly after the disturbance, we expected the similarity between the replicates exposed to the most intense disturbance to be the highest, due to the stronger filter effect of the disturbance and to the lower differences in species abundance between these replicates, which may homogenize the replicates' structure (Hypothesis 2) (Olsgard et al. 1998).

When considering the recovered communities within each biome, we expected that the similarity between the intensely disturbed replicates would be lower than the similarity between the lightly disturbed ones, since a more severe disturbance gives more opportunities to new colonizers, thus adding randomness to the communities (Hypothesis 3) (Zavaleta and Hulvey 2004).

Comparing the two biomes, we hypothesized that the recovered soil fauna communities would be more similar (regarding the compositional variation between sampling moments) to their pre-disturbed state in the boreal forest than in the temperate forest (Hypothesis 4). Our assumption was that deterministically driven species assembly after disturbances may be more important in boreal forests, where environmental conditions are constraining (Billings 1987), reinforcing the role of life-history traits for species to establish in this biome, than in temperate forests, where the milder environmental conditions may allow for more stochasticity to determine species assembly. Moreover, we expected the different replicates that had been lightly disturbed to be more similar to their pre-disturbed state than the intensely disturbed ones. This is due to the incumbency advantage new colonizers get from a more depopulated area (Hypothesis 5) (Thibault and Brown 2008).

Before testing these hypotheses, we analysed how to best calculate the dissimilarity between communities. Regarding our hypotheses, we computed the similarity index of the assemblages based on species abundances as well as abundances of diets, which is a commonly used trait of soil fauna (Rosenberg et al. 1986). The purpose was to be able to detect whether some communities, which appear taxonomically dissimilar, were in fact functionally similar (different species exhibiting the same functions).

Methods

Study sites

Fieldwork for the temperate deciduous forest took place in Klarenbeek, the Netherlands (52°10'49"N, 6°6'21"E), in a forest dominated by oak trees (Quercus robur); the ground was covered with a thick litter layer (5 to 10 cm). The boreal forest, situated in Rusutjärvi, Finland (60°27'2"N, 24°57'23"E), consisted of a mixed forest of spruces (Picea abies), birch trees (Betula pendula) and red pine trees (Pinus resinosa). The ground was mainly covered with grass, moss, ferns and cranberry shrubs. The climate of the two sites during the annual period of the Sampling I is presented in Table 1 of Chapter 2 (page 20). The ground of the boreal forest was covered with snow from late November till early April.

Sampling design

Sampling occurred following a randomized block design consisting of five blocks (i.e., replicates) of three treatment plots: a “control”, a “light disturbance” and an “intense disturbance” plot. To prevent pseudoreplication, these plots were separated by 20 m and blocks by at least 100 m. The disturbance was created by spraying the same brand and quality of diesel fuel on the ground of the two sites with a backpack sprayer: 50 ml/m2 for the light disturbance and 250 ml/m2 for the intense one. A trial experiment had been carried out by spraying various doses of diesel fuel on the litter layer: 50 ml/m2, 100 ml/m2, 250 ml/m2, 500 ml/m2, 1000 ml/m2; the smallest dose proved to be sufficient to significantly impact the macrofauna (50% decrease of the total abundance) and 250 ml/m2 decreased the total abundance to roughly 10% of the original one (results not shown). Sampling occurred four times in both biomes: three weeks before the disturbance (i.e., the reference, thereafter named Sampling I), giving enough time for the animals to recolonize before the disturbance, and then, one day, four months, and one year after the disturbance (respectively later on referred to as

Sampling II, III and IV). The first sampling occurred in May 2009 in the temperate forest and in June 2009 in the boreal one.

Soil Arthropods were collected by means of 10 cm-wide pitfall traps filled with 2 cm of salt saturated water as a preservative. A 20 cm-wide roof was placed 5 cm above the traps to protect them from the rain and direct sun. Plots were 100 m2 circles (5.6 m of radius) in which 12 pitfall traps were placed according to two sampling rings: an inner one, 2 m from the centre, and an outer one, 4 m from the centre (the six pitfall traps of each ring were evenly distributed along the circle they formed). The aim of this set up was to see whether the recovery would be due to animals recolonizing from the surrounding area (in which case the outer samples would have a higher abundance than the inner samples) or due to offspring of survivors (then, the species abundances of the samples of the inner and outer rings would be similar) (cf. Antunes et al. 2009). During the sampling time, pitfall traps were open for 10 days and each plot was surrounded by a 30 cm high plastic enclosure, of which 5 cm were buried belowground: this prevented animals from entering or leaving the plots during the sampling time, in order to obtain a better estimate of the abundance per unit area. At the end of each sampling session, samples were sieved into a strainer and rinsed to eliminate the salted water which was replaced by 70% ethanol for long term preservation.

Identification was undertaken with a stereoscopic microscope to the species or the family level. Morphospecies were sometimes used, based on the size (small, medium, large) of animals within some families (see Table 1 of Appendix 1). Owing to their scarcity and to taxonomic difficulties, larvae, pupae and nymphs were not taken into account. For some very numerous species groups, like ants, an estimation of the total number of individuals in some samples was undertaken, by counting a quarter of the animals evenly spread in a Petri dish.

Diets were attributed to species based on Hatteland & Hauge (2007), Ribera et al. (1999), Turin (2000), Loubère (2011) and according to Wim Dimmers and Theodoor Heijerman (pers. comm.). Each species was attributed one or more of the following diets: polyphagous, carnivorous, phytophagous, coprophagous, necrophagous, saprophagous and fungivorous.

Similarity index

There is a plethora of statistics meant to quantify how (dis)similar two (or more) ecological communities are (e.g., Legendre and Legendre 1998; Anderson et al. 2011). Because it takes abundances into account for comparisons of community composition (Pontasch and Brusven 1988; Ulrich and Zalewski 2006), we opted for the widely used Bray-Curtis dissimilarity index (Bray and Curtis 1957) (referred to as BC index thereafter) as defined by Legendre and Legendre (1998):

$$D(x_1, x_2) = \frac{\sum_{j=1}^{p} \left| y_{1j} - y_{2j} \right|}{\sum_{j=1}^{p} \left(y_{1j} + y_{2j} \right)}$$

where $D(x_1, x_2)$ is the Bray-Curtis dissimilarity index between sample x_1 and sample x_2, j the j^{th} species in a sample composed of a total of p species (p is the total species richness of samples x_1 and x_2 together), y_{1j} the abundance of species j in sample x_1 and y_{2j} the abundance of the same species in sample x_2. D is defined between 0 and 1, $D = 0$ indicating two exactly identical samples (zero dissimilarity), and $D = 1$, two samples which do not share any species (complete dissimilarity).

Several methods exist to transform and/or standardize the data (Whittaker 1978) before computing a similarity index. Although they have been widely used, they also have been shown to give different results than when using raw data (Olsgard et al. 1998; Yoshioka 2008). Among these methods, the most commonly used before computing a similarity index is the Wisconsin double standardization (referred to as DS thereafter), which was first introduced by Bray and Curtis (1957). Since there are some diverging opinions about the use of this standardization (Yoshioka 2008; Somerfield 2008), we decided to test it first.

We considered two groups (A and B) both composed of three samples. Each sample was made of ten different species and their abundances were randomly generated. Abundances of the three samples of group A were always defined between 0 and 100. Abundances of the three samples of group B were, at first, all defined between 0 and 100, then, according to the ranges shown in Table 1. In the first case of Table 1, when comparing the dissimilarity between the three samples of group A with the dissimilarity of the three samples of group B, they were expected to be, on average, equal. In the other cases, one could expect the dissimilarity between the three samples (of differing ranges) of group B to be higher than the dissimilarity of group A (composed of samples of equal ranges). To test for the influence of the DS on the BC index, we simulated the samples, using 100 000 runs, in order to compare the BC index of groups A and B in the different cases described above and shown in Table 1, with and without DS. The results showed that, in the first case (when the samples of both A and B ranged between 0 and 100), the BC index of group A was lower than group B's in 50% of the runs, with and without DS (Figure 1): there was an equal chance that the dissimilarity of one group was lower than the other's, as expected. As the difference between the ranges of the three samples of group B increased (and hence the dissimilarity of B increased compared to A), the percentage of runs for which group A's BC index without DS was lower also increased. However, the percentage of runs for which group A's BC index with DS was lower did not increase as much as without DS (Figure 1). This means that using DS increased the risk of failing to detect which group of samples was the most dissimilar; as the range difference between the samples increased, the risk was

Table 1: Abundance ranges of the three samples of groups A and B in the different cases tested.

	Group A			Group B		
	Sample 1	Sample 2	Sample 3	Sample 1	Sample 2	Sample 3
First case	0 → 100	0 → 100	0 → 100	0 → 100	0 → 100	0 → 100
Second case	0 → 100	0 → 100	0 → 100	0 → 100	0 → 125	0 → 150
Third case	0 → 100	0 → 100	0 → 100	0 → 100	0 → 150	0 → 200
Fourth case	0 → 100	0 → 100	0 → 100	0 → 100	0 → 200	0 → 300
Fifth case	0 → 100	0 → 100	0 → 100	0 → 100	0 → 1000	0 → 2000

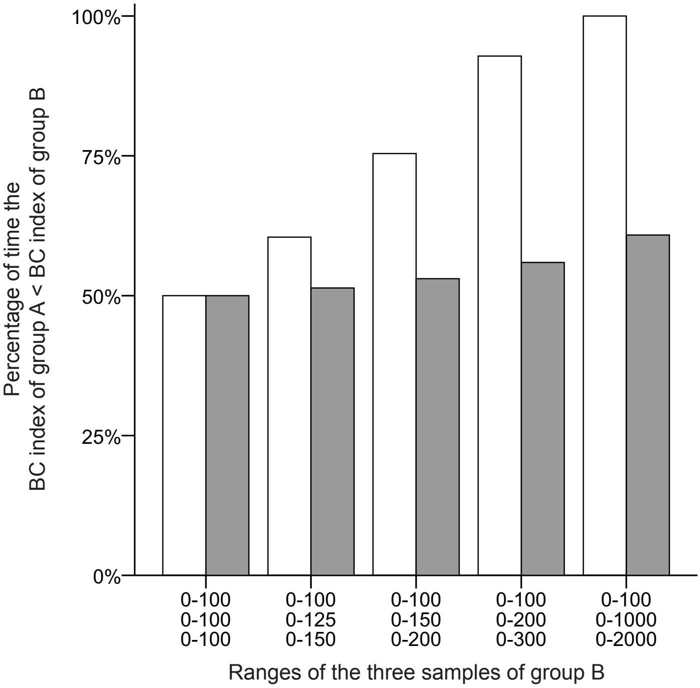

Figure 1: Percentage of 100 000 simulations that the Bray Curtis dissimilarity index of group A was lower than the BC index of group B (meaning that group A's samples are more similar than group B's) with and without using a Double Standardization. The three samples composing group A always have their abundances defined between 0 and 100, whereas the ranges of the abundances of the three samples of group B are increasingly different, as described on the x-axis.

greater (type II error). As the fact that our samples being heterogeneous in their total abundances and total abundances seemed highly probable in the case of a recovery, we decided to use the BC index without DS.

The BC index was computed with raw species abundances and diet abundances, the latter being calculated by binning the number of individuals of the species in their known diet(s) bin(s). Seven diets were used: polyphagous, carnivorous, phytophagous, saprophagous, coprophagous, necrophagous and fungivorous.

Statistics

Testing Hypothesis 1 required computing the BC index of the 15 samples of Sampling I for each biome. We used Anderson's method (2006), which runs a Principle Coordinate Analysis (PCoA) on the BC indices and calculates the distance of each point per group to its centroid before performing an ANOVA on these distances. This method was also used to test Hypotheses 2 and 3, respectively at Sampling II and IV. To test Hypotheses 4 and 5, we first computed the BC index (using the R package "vegan", Oksanen et al. 2011) for the five pairs of plots sampled during Sampling I and IV for each treatment of the two biomes, then tested the average BC index of these six groups (two biomes and three treatments) with a two-way ANOVA. We used one-sided tests given the expected one-sided differences, and therefore applied $\alpha = 0.1$.

Results

191 900 individuals were collected (38 511 in the temperate forest and 153 389 in the boreal forest) distributed among 14 families and 64 identified species (see Table 1 of Appendix 1). Total richness in the two biomes was similar, with respectively 55 and 53 species and morphospecies in the temperate and in the boreal forest (see also Comor et al. Chapter 2).

The BC index of all the 15 plots of each biome before the disturbance (Hypothesis 1) was higher in the boreal forest (higher β-diversity) than in the temperate forest, both for the species ($F_{1,28} = 21.25$, $P < 0.001$) and the diet abundances ($F_{1,28} = 39.35$, $P < 0.001$). Figure 2.A shows that the boreal communities, based on the species abundances, are more spread apart than the temperate ones.

After the disturbance, the results of the ANOVAs performed on BC indices showed that lightly disturbed plots had equal similarities to intensely disturbed plots in either biome (Hypothesis 2; Table 2; Figure 2.B). The similarity of the similarly-treated plots at their recovered state (Sampling IV) did not differ either between the different treatments in both biomes (Hypothesis 3; Table 2; Figure 2.C).

The dissimilarity of the disturbed communities of each plot before (Sampling I) and one year after (Sampling IV) the disturbance, based on the species abundances, was higher in the temperate forest (Hypothesis 4), but there were no differences between the treatments within each biome (Hypothesis 5) (two-way ANOVA: Treatment $F_{2,24} = 1.51$, $P = 0.241$; Biome $F_{1,24} = 3.47$, $P = 0.075$; Biome x Treatment $F_{2,24} = 0.20$,

Table 2: Abundance ranges of the three samples of groups A and B in the different cases tested.

Hypothesis	Biome	Abundance	F	*P*
2 (Sampling II)	Temperate	Species	$F_{2,12} = 0.291$	0.753
		Diets	$F_{2,12} = 0.427$	0.662
	Boreal	Species	$F_{2,12} = 1.162$	0.346
		Diets	$F_{2,12} = 1.540$	0.254
3 (Sampling IV)	Temperate	Species	$F_{2,12} = 0.104$	0.906
		Diets	$F_{2,12} = 0.240$	0.773
	Boreal	Species	$F_{2,12} = 0.004$	0.996
		Diets	$F_{2,12} = 0.074$	0.839

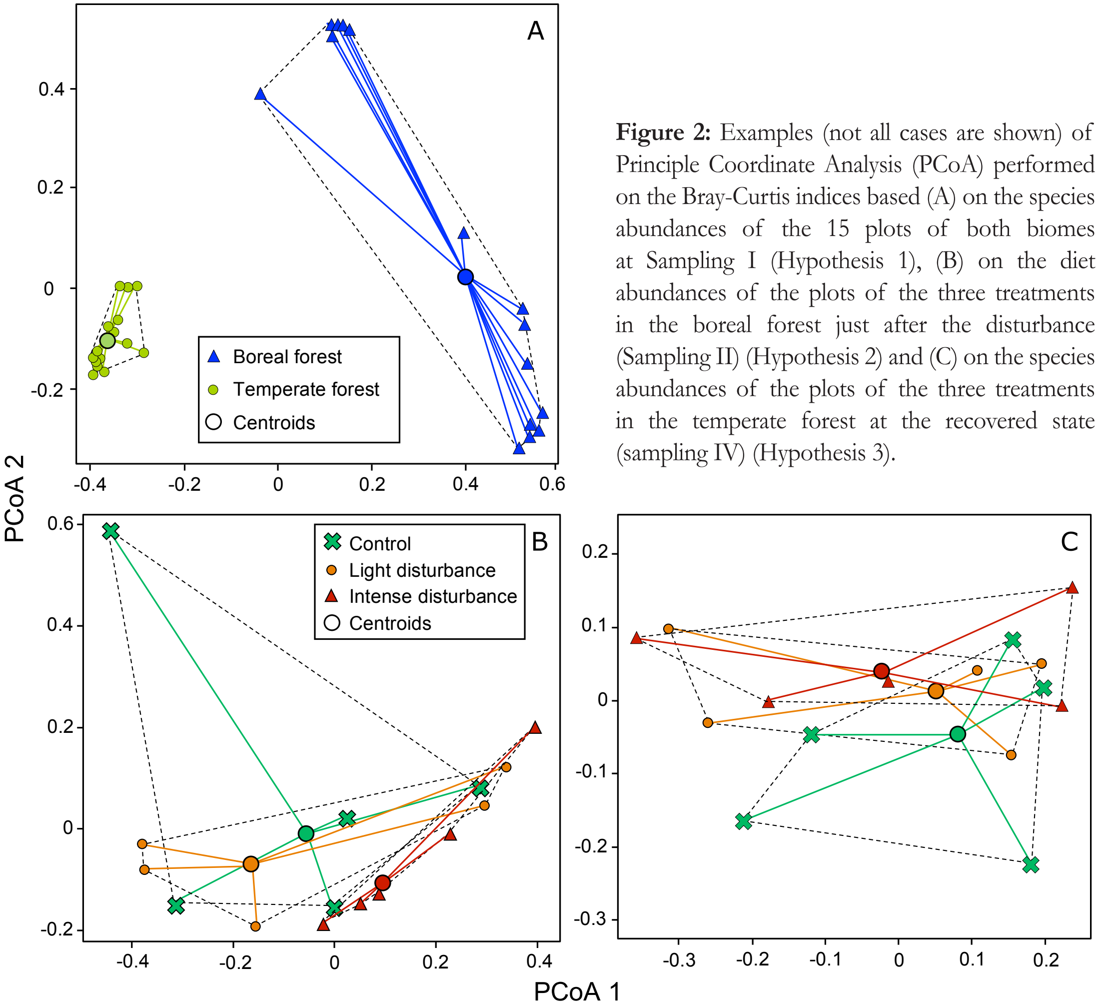

Figure 2: Examples (not all cases are shown) of Principle Coordinate Analysis (PCoA) performed on the Bray-Curtis indices based (A) on the species abundances of the 15 plots of both biomes at Sampling I (Hypothesis 1), (B) on the diet abundances of the plots of the three treatments in the boreal forest just after the disturbance (Sampling II) (Hypothesis 2) and (C) on the species abundances of the plots of the three treatments in the temperate forest at the recovered state (sampling IV) (Hypothesis 3).

$P = 0.819$) (Figure 3.A and 3.B). There were no differences for the same analyses based on the diet abundances (two-way ANOVA: Treatment $F_{2,24} = 0.75$, $P = 0.482$; Biome $F_{1,24} = 0.45$, $P = 0.510$; Biome x Treatment $F_{2,24} = 0.01$, $P = 0.996$).

DISCUSSION

This study compares, for the first time, species assembly between two biomes with contrasting environmental conditions in order to determine whether species assembly follows the predictions from the niche or neutral theory. To test the predictions of these theories, we disturbed soil fauna communities in these biomes and recorded their recovery. As we assumed that deterministically driven species assembly may be more important in boreal forests where environmental conditions are constraining (Chase 2010), we hypothesized that the recovered soil fauna communities would be more similar to their pre-disturbed state in the boreal forest than in the temperate forest (Hypothesis 4). Our results show indeed that the dissimilarity of all the soil fauna

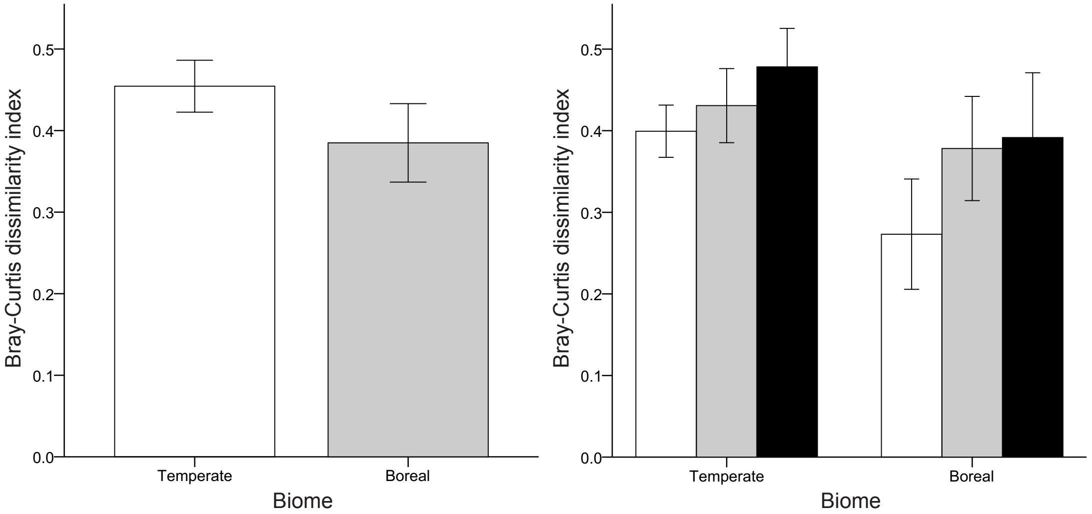

Figure 3: Estimated marginal means of the Bray-Curtis dissimilarity indices (±1SE) based on the species abundances of the same plot at Sampling I and Sampling IV A) between the boreal and the temperate biomes, including all the treatments (Hypothesis 4), with the BC index significantly higher in the temperate forest (P = 0.075), and B) between the three treatments in both biomes (Hypothesis 5) (letters indicate significant differences between treatments).

communities, based on their species abundances before and after the disturbance, was higher in the temperate forest than in the boreal forest (higher compositional variation across sampling moments, Figure 3.A). In places where environmental conditions are constraining, life-history traits for species to establish may play a more prominent role, whereas the milder environmental conditions in the temperate forest may allow for more stochastically driven species assembly. Although we expected differences between the treatments (Hypothesis 5), none was found (Figure 3.B). These results suggest that the soil fauna communities recovered in both biomes after one year (Comor et al. Chapter 2) and that, even without a disturbance, the structure of the soil fauna communities in the boreal forest would not change much from one year to another: during the growing season, these boreal communities assemble similarly to their previous structure (before winter). Studying soil fauna in a temperate forest, Berg and Bengtsson (2007) found that the seasonal variability was higher than the interannual one. Korhonen et al. (2010), who studied aquatic systems, confirmed this trend but found that interannual variation was higher at higher latitudes, contradicting our results. When we considered species life-history traits, our analyses did not reveal any difference between the two biomes. We expected the analysis of traits to show clearer results than species abundances as they are the factor directly responding to environmental conditions (Grime 2006), but our limited diversity of traits (only seven diets) may be the cause of the lack of any observable pattern. Berg and Bengtsson's study confirms our results which could also be explained by trait redundancy among species assemblages, where different species have some similar life-history traits.

Although we expected the initial dissimilarity between all plots (β-diversity) to be higher in the temperate forest than in the boreal forest (Hypothesis 1), we found the opposite (Figure 2.A). The more constraining environmental conditions of the boreal biome did not impede variation between communities and the temperate forest showed surprisingly little variation from one community to another. This higher dissimilarity between the boreal assemblages could not be related to higher species richness, as species richness was equal in both biomes, nor to more diverse flora (trees, understory), litter or soil conditions in that biome: organic matter content (92% w/w in the temperate forest and 93% w/w in the boreal forest), percentages of carbon (47% w/w in both forests), nitrogen (2% w/w in both forests) and phosphorus (0.1% w/w in both forests), as well as pH (4.6 in both forests, measured from the dried litter) were equal in both biomes (see Comor et al. Chapter 1). The irregular abundance of ants from plot to plot in the boreal forest could also not explain the higher dissimilarity, as the same analysis performed without the ants in both biomes produced similar results. A common cause of community dissimilarity (high β-diversity) is dispersal limitation (Hubbell 2001), but it is unlikely that this might explain our results as there were no barriers which could have separated the different communities, unlike in the case of Barber and Marquis (2011) who found distance from one herbivore insect tree community to another to be the only factor influencing community composition. Chase et al. (2009) showed that predation could increase the similarity between communities, acting as an ecological filter, but we cannot justify a higher predatory pressure in the temperate forest than in the boreal forest. According to Kucharik et al.'s data (2000), the net primary productivity is 0.693 kg C/m2/year in the temperate study area and 0.535 kg C/m2/year in the boreal one; hence, the lower primary productivity cannot explain the higher dissimilarity (higher β-diversity) in the boreal forest either (in contrast to the findings of Chase 2010).

Although these findings about similarity across local sites (β-diversity, Hypothesis 1) contradict the findings about similarity between sampling moments (Hypothesis 4), we found that species assembly after a disturbance in more constraining environments, such as boreal forests, may be more deterministically driven than in less constraining environments, such as temperate forests, which is also found by Chase (2010).

Evidence for stochastic processes underlying species assembly comes from relatively productive environments such as tropical rainforest and coral reefs (Hubbell 2001; Condit et al. 2002; Latimer et al. 2005; Volkov et al. 2007), whereas deterministic processes may play a stronger role in less productive environments such as temperate forests (Clark and Mclachlan 2003; Gilbert and Lechowicz 2004). The importance of traits is supported by other studies on soil fauna that have shown that these assemblages seem to be rather niche-driven: species are specialised depending on micro-habitat (Usher et al. 1982), with a productivity strongly related to the quality rather than the quantity of organic matter (Rushton and Hassall 1987), which controls the diversity of higher trophic levels (Wardle 2002). It would be interesting to reproduce our experiment in environments in which stochastic processes have been mainly found, such as in tropical forests.

Just after the disturbance, there was no difference between the similarity of the communities which received a different treatment (Hypothesis 2; Figure 2.B). There was also no difference between the treatments when compared to their pre-disturbed state (Hypothesis 5; Figure 3.B), even though the disturbance had a great impact on the abundance of the boreal communities (Comor et al. Chapter 1). The disturbance thus did not have the expected homogenizing effect because it may have acted randomly.

To date, studies focusing on species assembly and community similarity have mainly been carried out on plants with experimental plots (Fukami et al. 2005; Grime 2006; Cornwell et al. 2006). Our study based on fauna emphasizes the need to disentangle the temporal from the spatial scale in community assembly.

Tests of niche versus neutral models have been conducted in a wide variety of ecosystems, varying from tropical forests (Hubbell 2001; Condit et al. 2002; Volkov et al. 2007), temperate forests (Gilbert and Lechowicz 2004), grasslands (Adler 2004) and marine ecosystems (Wootton 2005). While some of these tests tended to support either niche or neutral models, in most cases the results were intermediate (Gravel et al. 2006). In this paper, we test the predictions of both models in two climatically contrasting environments, as climate (or energy) might determine the continuum between niche and neutral theory (Chase 2007; 2010). In these two biomes, we tested the predictions by disturbing soil fauna communities and investigated their recovery. Disturbances often lead to changes in community properties such as species richness or abundances of species. Many studies which have examined how disturbance affects communities have focused on how average values of these properties change with disturbance (Murphy and Romanuk 2012), but the community response of disturbances can also be measured as the variation among replicates after the disturbance (Mcgrady-Steed et al. 1997; Carpenter and Brock 2006; Forrest and Arnott 2007). In this paper, we show that among replicate variation, and hence the predictability of the community response, might depend on environmental conditions. In low-productive environments, the response to disturbances might be less variable, thus more predictable (following the niche theory), than in high-productive environments. Our results contribute to understanding the community responses after disturbances and the role of environmental conditions.

Acknowledgements

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CHAPTER 4

Changes in the density – body mass relationship of soil fauna after a disturbance

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Abstract

Theory on the density – body mass (DBM) relationship predicts that when the body mass of animal species increases, their density decreases with body mass to the power -0.75. The slope of this relationship is however largely debated. We tested the ability of the DBM relationship to reflect changes in the structure of communities subjected to a disturbance. We hypothesized that the slope of the DBM relationship would become less steep if mainly small animals were impacted by the disturbance and that, alternatively, the slope would become steeper if mainly large animals were affected. We sampled soil fauna from a semi-arid grassland before and after spraying diesel fuel. Results showed that the slope became less steep just after the disturbance, because the impact was mainly on smaller fauna and the first colonizers had high body mass. Our findings show that the response of communities to changing environmental conditions provides an alternative explanation for the large variation in observed slopes of the DBM relationship, and that multiple sampling moments are needed to avoid temporal artefacts of community composition in establishing the DBM relationship. When the DBM relationship varies predictably after a disturbance, our findings suggest that it can be used for biomonitoring.

INTRODUCTION

Understanding the density of organisms is a key challenge in ecology (Gaston and Blackburn 2000). There is extensive empirical evidence for negative scaling of species density in relation to their body size, i.e., the density – body mass relationship (hereafter referred to as DBM relationship) (Elton 1927; Mohr 1940; Damuth 1981, 1987; Duarte et al. 1987; Enquist et al. 1998). Theory predicts a negative relationship between species density (D) and body mass (M) described as a power law $D = a \cdot Mb$, where the exponent b is approximately −0.75 for taxa within a single trophic level (Nee et al. 1991; West et al. 1997; Brown et al. 2004). Across trophic levels, an exponent b of −1 is widely reported (Peters and Wassenberg 1983; Boudreau and Dickie 1992; Schmid et al. 2000). However, these exponents are not always found (White et al. 2007), and even positive relationships (Russo et al. 2003; Maxwell and Jennings 2006) or no relationship (e.g., Gaston and Lawton 1988) have been observed. Other shapes of the DBM relationship have been found too, such as a polygonal relationship (Brown and Maurer 1987; Cotgreave 1993; Leaper and Raffaelli 1999; Andrew and Hughes 2008). Different explanations have been given for the range of slopes of the DBM relationship, such as too narrow body size ranges (Brown and Maurer 1987; Morse et al. 1988; Silva and Downing 1994; Cyr et al. 1997a), sampling artefacts (Lawton 1989; Arneberg and Andersen 2003) and sampling species within only one taxon (Schmid et al. 2000).

When a community is subjected to environmental modifications, for instance due to disturbances, its DBM relationship is expected to reflect this variation (Cyr et al. 1997b; Siqueira et al. 2008; Reuman et al. 2009) because of the changes in density and species composition (and hence, changes in body mass distribution) of the community (Leaper and Raffaelli 1999). For instance, the ability to reproduce fast, a high tolerance to disturbance agents, a particular diet or fast dispersal capabilities (Sousa 1984) are traits that allow organisms to (re)colonize a disturbed system. Given that many of these traits are related to body mass (Peters 1983), the DBM relationship of such a disturbed system may divert from its predicted slope. The response of communities to changing environmental conditions could thus provide an explanation for the large variation in observed slopes of the DBM relationship. We therefore experimentally tested the effect of changing conditions on the slope of the DBM relationship by exposing soil fauna communities to a disturbance and monitored the community composition before and after the disturbance. Such experimental study to test the DBM relationship in which a disturbance is applied, and body mass and densities are measured at various times after the disturbance, is lacking to date (Reuman et al. 2009).

We previously showed that a disturbed soil fauna community returns to its initial state which is at least functionally similar (Comor et al. Chapter 3). Therefore, we expected that, when heavily disturbed, the slope of the DBM relationship in a soil fauna community would have a different slope than before the disturbance, and that the slope would return to its initial value as the community recovers. With regard to the direction the slope would take after the disturbance, we tested two alternative hypotheses

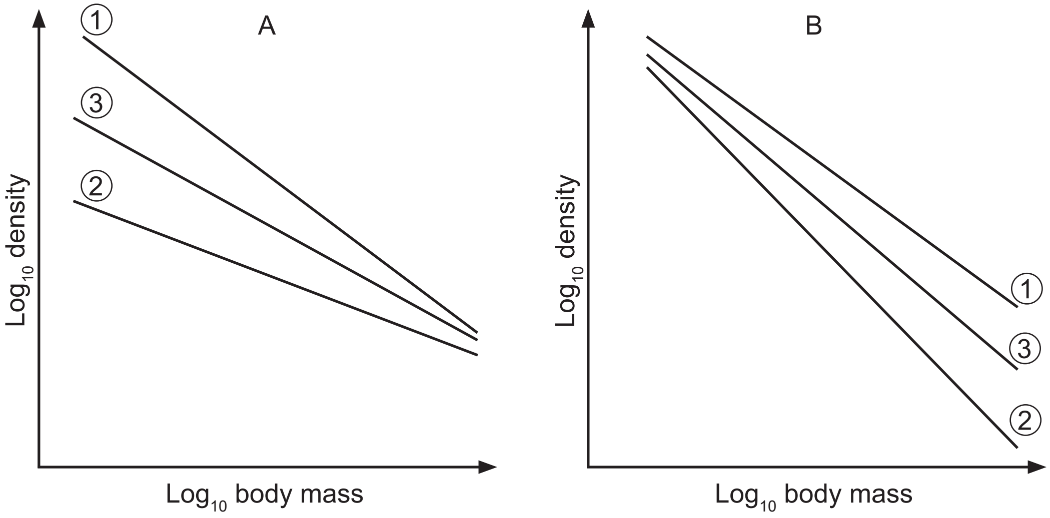

Figure 1: Expected slopes of the density – body mass relationship: ① before the disturbance, ② just after the disturbance and ③ during the recovery, (A) where small animals are more impacted than large ones (Cyr et al. 1997a) and (B) where large animals are more impacted than small ones (Reuman et al. 2009).

depending on which body mass categories are mostly impacted by the disturbance: if smaller animal species suffered more from the disturbance than larger ones, then the slope would be more positive after the disturbance (shallower slope, Figure 1.A) (Cyr et al. 1997a), but if larger animal species were more impacted than smaller ones, then the slope would be more negative (steeper slope, Figure 1.B) (Reuman et al. 2009). To test these hypotheses, we sampled a wide range of soil fauna organisms including animals as small as nematodes and as big as carabid beetles spanning seven orders of magnitude. We used the local size-density relationship (LSDR) to analyse the slope of the DBM relationship (Reuman et al. 2008).

Sampling was focussed on three main groups of soil fauna: nematodes, Collembola and larger arthropods. Nematodes are part of the diet of Collembola (Gilmore and Potter 1993), which are part of the diet of other arthropods (Coleman et al. 2004), linking these three groups in a food chain. Arthropods are also an important source of food of larger animals. Knowing which size classes are impacted by a disturbance is relevant for understanding the impact on community structure and functioning as predator often choose their prey according to their size (Simon 1976; Sherry and McDade 1982; Pearson and Derr 1986; Greenberg and McGrane 1996). These three groups of animals are known to respond to disturbances and to rapidly recover as well (Rosenberg et al. 1986; Brmez et al. 2008; Zeppelini et al. 2009). In order to create a pulse disturbance that would allow for a rapid recovery, we used diesel fuel: it is toxic to these animals (The Shell Company of Australia Ltd 2010) and does not damage their habitat (Comor et al. Chapter 2).

Methods

Experimental design

Field work took place in Wits Rural Facility, Hoedspruit, Limpopo Province, South Africa (24°15’20.23”S, 31°23’23.63”E) during the wet season from November 2009 until January 2010. The area is covered with savanna vegetation and it is part of the Granite Lowveld region (Mucina and Rutherford 2006). The average climate of the area is classified as semi-arid under the Köppen-Geiger System (Kottek et al. 2006). The long-term mean yearly rainfall is about 438 mm, the mean maximum temperature during January (hottest month) is 33.7°C and the mean minimum temperature in June (coolest month) is 9.4°C (Venter et al. 2003).

We applied a randomized block design. Ten blocks at least ten metres away from one another were chosen so that they shared similar vegetation and soil type: grassland, no shrubs or trees, 30 cm sand before clay. Each block had three plots of 3 × 3 m, separated by at least 5 m, with different treatments: a control, a light disturbance and an intense disturbance. The disturbance was created by spraying diesel fuel with a backpack sprayer onto the surface of the ground, with doses known to impact soil and litter fauna (Comor et al. Chapter 2): 100 ml.m^{-2} for the light disturbance and 200 ml.m^{-2} for the intense one. In these plots, we sampled soil fauna four times: three weeks before the disturbance (Sampling I), one day after the disturbance (Sampling II), and again one month (Sampling III) and two months (Sampling IV) after the disturbance.

To sample arthropods, five pitfall traps per plot, 13 cm deep and 9 cm wide (to decrease the bias toward high-body mass species, Ulrich et al. 2005) were open for three days at each sampling moment, with 2 cm of salt-saturated water as a preservative. Collembola were sampled by collecting four cores per plot of the first 5 cm of the soil with a 4.1 cm auger. Samples were then extracted in Tullgren funnels for two weeks. Nematodes were sampled by collecting six cores of soil per plot with a 1.5 cm wide auger to a depth of 10 cm. These samples were then gently mixed together and 120 ml of soil were used for the subsequent extraction, following Cobb’s method (Cobb 1918; van Bezooijen 2006).

Body mass determination

The animals collected in the pitfall traps were soaked in water and rinsed to eliminate the salt, dried 70°C for 48 hours and weighed with a microscale (precision of 1 μg). With regard to Collembola and nematodes, 100 individuals of each group, regardless which species, were dried at 70°C for 48 hours and weighed together (each group separately) with the same microscale to obtain an estimation of the average weight of one nematode and one springtail. The results were that the average weight was 57.5 μg for one springtail and 0.295 μg for one nematode (which corresponds to what has been reported in the literature; Fjellberg 1998, 2007; Tita et al. 1999).

Body mass classes of nematodes, Collembola and larger arthropods were defined based on the $\log_{10}$(body mass in grams). Each class corresponded to a quarter of one $\log_{10}$(body mass in grams) unit, with the first class being −6.74 to −6.50, then −6.49 to −6.25, and so on until the last class, 0.24 to 0.50. Nematodes all belonged to the first class and Collembola to the class −4.24 to −4.00. The animals caught in the pitfall traps were spread in 12 classes between −3 and 0.50 (see Table 1 of Appendix 2).

Calculation of densities

Total abundances of animals were converted into densities in number of individuals.m^{-2} to allow for comparisons. The abundance of Collembola and nematodes was not considered relative to a volume, but to surface area, since most of these animals live in the first few centimetres of the soil.

For each sampling moment and for each weight class, total abundances of all the pitfall traps of each treatment (5 pitfall traps × 10 plots = 50 pitfall traps) were divided by the sampling area, i.e., 90 m^2 (10 plots of $9m^2$), that was considered to be covered by the pitfall traps. We could not use fences around the plots to directly obtain densities because of the large herbivores roaming the area, which would have destroyed these fences (see below the test for the size of the sampling area). Densities of Collembola were calculated based on the surface area of the corer (58.81 cm^2), representing 211.24 cm^2 for four samples. Hence, we multiplied the total abundance of Collembola of the four samples by 47.34 to obtain the number of individuals.m^{-2}. Regarding nematodes, the volume of compact soil sampled in six cores (106 cm^3) represented a volume of 212 cm^3 of loose soil, of which 120 cm^3 were used for the extraction. The total abundance of nematodes in six cores was thus 1.77 times the one in 120 cm^3 of soil. The six cores represented a surface area of 10.60 cm^2, therefore we multiplied the nematode abundance of the six cores by 943.14 to obtain the density in number of individuals.m^{-2}.

Statistical analyses

The slopes of the DBM relationships were calculated both by Reduced Major Axis (RMA) regression (Griffiths 1992), using Software for RMA Regression (Bohonak and van der Linde 2004), and by Ordinary Least Square (OLS) regression. Since there were only marginal differences between the results of the two regression methods, we opted for the OLS, as it offers the possibility to easily perform statistical analyses on the slopes (see Table 2 of Appendix 2 for the results of the RMA regressions).

In order to verify the validity of the assumption that the sampling area for calculating the densities of the arthropods covered $9m^2$ (3×3m plots), we also computed the DBM relationships with the same total abundances but with plot sizes of $6m^2$ and $12m^2$, to see how much variation there was between the slopes of the DBM relationships (the values of the densities of nematodes and Collembola were kept the same for each density of arthropods per sampling, as these ones were known). Then, we used General

Linear Models (GLMs) to test for differences between the slopes of the three densities for each sampling, with the animal densities as the dependent variable, the three levels of densities as fixed factor and body mass as covariate. As the results clearly showed that there was no difference between the slopes obtained with the three sampling areas considered to calculate arthropod densities (see Table 3 of Appendix 2), we chose to use the densities of pitfall trap arthropods based on 9m^2 for the following analyses.

Testing the differences between the treatments for each sampling was also carried out with GLMs, with the animal densities as the dependent variable, the treatments as fixed factor and body mass as covariate. When the GLMs detected a significant difference between the three slopes of one sampling moment, we tested for the differences between the slopes using a Sidak post hoc test.

RESULTS

A total of 22 535 nematodes, 721 Collembola and 6575 arthropods were collected, from which the densities of each body mass class were determined (Table 1 of Appendix 2). Before the disturbance, the slopes of the DBM relationships of the three treatments were almost perfectly parallel, with slopes around −1 that did not differ significantly between each other (Figure 2.A, Figure 3, Table 1). Just after the disturbance (Sampling II), the slope of the DBM relationship of the intensely disturbed plots increased from −1 to −0.72, the slope of the lightly disturbed plots increased from −1 to −0.93 and the slope of the control plots remained similar (Figure 2.B). The slope of the intensely disturbed plots was significantly higher than the one of the two other treatments (Table 1). One month after the disturbance (Sampling III), the slopes of the disturbed plots continued

Table 1: Results of the GLMs on the slope elevations of the DBM relationships of the three treatments for each sampling (left-hand side) and the post hoc Sidak tests on the three pairwise combinations of the three treatments for the significant interactions (right-hand side). Significant values are bolded.

Sampling	Source	*P*
I	Treatment	0.899
	Body Mass	< 0.001
	Treatment × Body Mass	0.998
II	Treatment	0.725
	Body Mass	< 0.001
	Treatment × Body Mass	**0.004**
III	Treatment	0.137
	Body Mass	< 0.001
	Treatment × Body Mass	**0.004**
IV	Treatment	0.703
	Body Mass	< 0.001
	Treatment × Body Mass	0.207

Pairwise comparisons	*P*
Control vs. Light	0.200
Control vs. Intense	**0.001**
Light vs. Intense	**0.028**
Control vs. Light	**0.026**
Control vs. Intense	**0.001**
Light vs. Intense	0.227

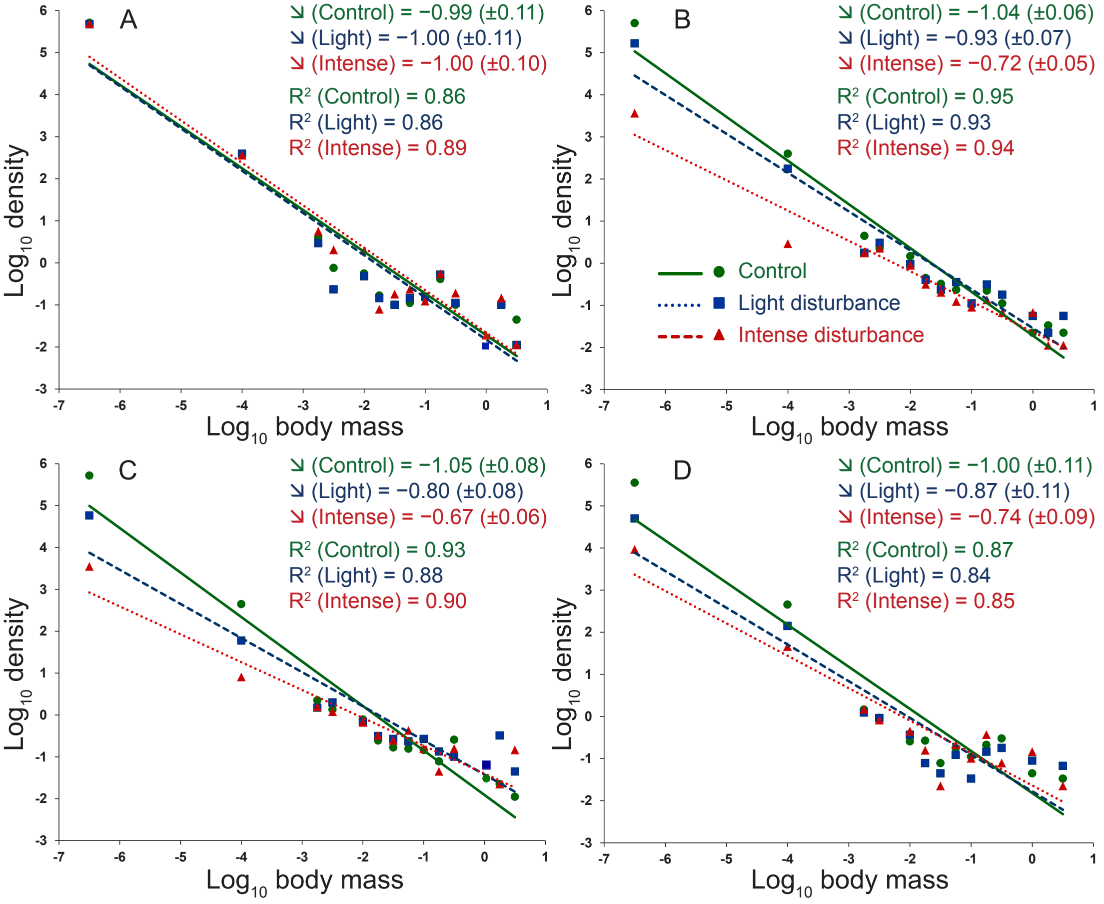

Figure 2: Log$_{10}$ Density – Log$_{10}$ Body mass relationship of all the animals collected in the three treatments and at (A) Sampling I, (B) Sampling II, (C) Sampling III and (D) Sampling IV. ↘: slope of the density body mass relationship (±1SE). R²: adjusted R².

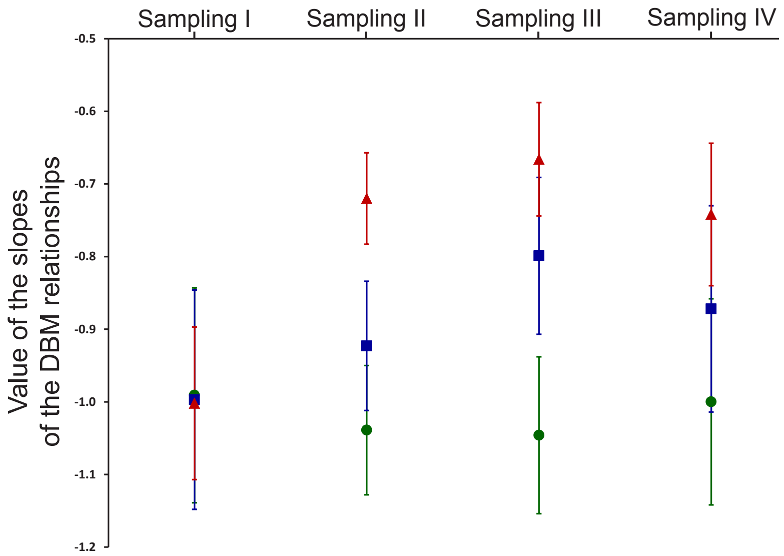

Figure 3: Changes in the slope of the DBM relationship (±1SE) for the three treatments from Sampling I to Sampling IV, calculated by reduced major axis regression. Letters indicate differences between treatments within a sampling.

to increase, with the intensely disturbed one reaching −0.67 and the lightly disturbed one −0.80, while the control slope remained around −1 (Figure 2.C). Both slopes of the disturbed plots were significantly higher than the control at Sampling III (Table 1). Only after two months (Sampling IV), the slopes of the disturbed plots started to decrease (Figure 2.D). There were no significant differences between the treatments anymore (Table 1). The changes of the slopes during the four sampling moments showed that the DBM relationship of the disturbed communities increased after the disturbance, peaked at Sampling III, while the control remained stable (Figure 3).

At Sampling II, the density of Collembola (with a $\log_{10}$(body mass) of −4) dropped proportionally more than the densities of animals of other body mass classes (Figure 2.B). The largest arthropods present in the intensely disturbed plots at Sampling I (Figure 2.A) appear to be less numerous just after the disturbance (Figure 2.B). However, these large arthropods were in higher number at Sampling III (Figure 2.C), thus contributing to the increase of the slope.

Discussion

In this paper, we experimentally tested the effect of a disturbance on the slope of the DBM relationship of soil fauna communities. We showed that the DBM relationship responds to changing environmental conditions, in our case, a disturbance. We found support for the hypothesis that the slope is more positive after a disturbance (shallower slope, Figure 1.A) (Cyr et al. 1997a) suggesting that smaller animals suffer more from this disturbance than larger ones. The disturbed communities showed a larger slope, confirming previous findings that steeper (more negative) slopes characterize more stable environments (Cyr et al. 1997a; Jennings and Mackinson 2003). As can be expected, the effect of the intense disturbance on the change in slope of the DBM relationship was larger than the effect of the light disturbance. Our results show that the response of communities to changing environmental conditions could thus provide an explanation for the large variation in observed slopes of the DBM relationship. Linking the DBM relationship to environmental conditions and variations in these conditions in a controlled experiment has not been done before (Reuman et al. 2009), although the DBM relationship's components are directly related to an often used community characteristic, density of species, and to an often measured species trait, body mass (Lawton 1990; Saint-Germain et al. 2007).

The smaller animals, especially the Collembola, seem to have been more impacted just after the disturbance than the other groups of animals (Figure 2.B). This could be explained by the fact that they live very close to the surface and are known to be organisms more sensitive to disturbances, often used as biological indicators in polluted areas (Zeppelini et al. 2009). Nematodes, even though they are highly sensitive to disturbances as well (Bongers and Bongers 1998), live deeper in the soil and are thus more protected from aboveground disturbances. At Sampling III (i.e., early recovery stage), the slope of the DBM relationship continued to increase, not because the disturbance was still impacting the communities, but probably because of the early colonizers; their good dispersal capabilities, which are related to high body mass (Brown et al. 2004; Jenkins et al. 2007), allowed them to rapidly reach the new potential habitat (Comor et al. Chapter 3) and skewed the slope toward more positive values. Reuman et al. (2009) also found that variations of the slope could be explained by environmental factors (anthropogenic and natural), but found steeper slopes in the most disturbed systems, due to the lack of large animals in disturbed areas.

Contrary to studies on a narrow range of animals or even on a single taxon (e.g., Brown and Maurer 1987 on birds; Morse et al. 1988 on arboreal tropical beetles; Silva and Downing 1994 on mammals; Russo et al. 2003 on tropical birds; Ulrich et al. 2005 on ground beetles), our data contained several levels of the food chain in soil and litter fauna due to the use of different sampling methods, resulting in several orders of magnitude of body mass. This sampling allowed to avoid common mistakes, such as a sampling bias toward the most abundant species (Lawton 1989) and a sampling artefact described by Arneberg and Andersen (2003) when using only one sampling method. Our multiple sampling methods of local communities took into account rare species (Blackburn et al. 1993) as well as small ones (Stork and Blackburn 1993), usually omitted, though relevant to these studies. This approach may have allowed us to detect changes in the DBM relationship due to changes in environmental conditions (Stork and Blackburn 1993; Cyr et al. 1997a, 1997b). Besides the necessary extension of the sampling to a wide range of body masses, our results also suggest to use multiple sampling moments, in order to avoid mistakes due to temporal artefacts (Cyr et al. 1997b), as our study shows that temporal changes in environmental conditions could lead to different slopes of the DBM relationship.

The value of the slope of the DBM relationship across trophic levels has been shown to be −1 (Peters and Wassenberg 1983; Boudreau and Dickie 1992; Schmid et al. 2000). Our results corroborate these findings as we found slope values between −1.05 and −0.99 in the control communities. This is steeper than the predicted −0.75 that underlies the "energetic equivalence rule" (EER) (Nee et al. 1991). This EER states that, if the DBM relationship has indeed a slope of −0.75, and given that the individual metabolic rate increases across body mass with an exponent $b = +0.75$, then population energy use per unit area (the product of density and individual metabolic requirements) is approximately independent of body mass. Several studies found support for the EER (Marquet et al. 1995; Medel et al. 1995; Ernest et al. 2003), whereas others did not (Hayward et al. 2009). The latter study is the only one that examined the EER in a community of naturally coexisting species at local scales of observation. Although the DBM relationship at local scales can be highly variable (White et al. 2007), we found values for the slope of −1 as expected for communities that contain several trophic levels (Schmid et al. 2000). Our results support the suggestion that no single energetic rule can account for the patterns in different taxonomic groups.

As body mass of species is related to many other traits (Peters 1983; Peterson et al. 1998; Lewis et al. 2008), i.e., physiological, behavioural and ecological characteristics of an animal (Damuth 1987), it is suggested that body mass provides predictive capabilities for environmental biomonitoring (Cyr et al. 1997b; Layman et al. 2005). When the DBM relationship varies predictably after a disturbance, we argue that the DBM relationship measured at the scale of a community could be an indicator of the state and health of a system by providing information about its structure. Both density differences and body mass spectra are valuable in comparing large-scale structural patterns among ecological communities and, because they include information both on the size of organisms and on community biomass, they are intimately tied to ecosystem function (Cyr et al. 1997b; Brown et al. 2004).

This study is the first to demonstrate experimentally that a system, when disturbed, shows a different DBM relationship than before. As the DBM relationship is based on one of the most representative traits in community ecology, body mass, we show that it can reflect the structure and functioning of a community. Moreover, it provides an estimate of a community's body mass distribution and its fluctuations due to changing environmental conditions, which may give insight into how energy is partitioned among species in communities, a fundamental question in ecology (Andrew and Hughes 2008).

Acknowledgements

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CHAPTER 5

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 plant and animal communities. According to the species – energy hypothesis, species abundance and richness are expected to increase as productivity increases, but it is still not clear which trophic levels benefit from higher productivity. As the density – body mass (DBM) relationship has been shown to reflect changes in the structure of communities subjected to environmental modifications, we propose to use it to better understand the influence of low and high productivity on soil fauna communities, with an additional disturbing factor: cattle grazing. We hypothesized that either; all the trophic levels would benefit from higher productivity, reflected by a higher Y-intercept of the DBM relationship; only smaller animals would benefit, reflected by a lower slope of the DBM relationship; only larger animals would benefit, reflected by a higher slope of the DBM relationship. We also supposed that communities subjected to grazing would have a lower DBM relationship compared to non-grazed ones. To test this, we collected a large range of soil fauna from different elevation levels of a salt marsh, thence from varying levels of productivity (due to the sea inundation frequency), in grazed and ungrazed areas. Differences in litter biomass were used to represent different levels of productivity, with the most inundated areas expected to be less productive. Only the DBM relationships of the most and least frequently inundated ungrazed sites were different, confirming that high-productivity communities have a lower DBM relationship slope, but no slopes differed regarding grazing. We conclude by suggesting that high productivity does not equally affect the different trophic levels and that the equivalence energy relationship may stand for within-trophic-level comparisons, but may fail for between-trophic-level comparisons due to inefficient transfers of energy from one trophic level to another

INTRODUCTION

It is generally accepted that the productivity of ecosystems has a large effect on the composition and structure of the plant and animal communities in these ecosystems (Evans et al., 2005; Gillman and Wright, 2006; Waide et al., 1999). According to the species – energy hypothesis, species abundance and richness are expected to increase with productivity (Wright et al., 1993). However, the mechanisms underlying these patterns remain unclear to date (Adler et al., 2011; Gillman and Wright, 2006). For example, increases in resource availability are expected to affect all trophic levels in a food web by increasing species richness and abundances, but higher trophic levels might not always benefit from higher productivity at lower trophic levels as consumer responses to resource subsidies will be lower at higher trophic levels (Abrams, 1993; Marczak et al., 2007). Moreover, the relationships between species richness and productivity may take a number of forms, due to the influence of factors such as spatial scale (Chase and Leibold, 2002), but they almost invariably include a strong positive phase (Evans et al., 2008; Mittelbach et al., 2001; Waide et al., 1999; Whittaker and Heegaard, 2003). Disturbance is another factor influencing the composition and structure of communities, of which the effect is debated: some studies suggest a unimodal relationship between diversity and disturbance, whereas others found positive or negative relationships (Mackey and Currie, 2001; Shea et al., 2004). This relationship can be influenced by the level of ecosystem productivity (Haddad et al., 2008; Kondoh, 2001).

The functioning of a community, and consequently its responses to productivity and disturbance, is determined by species-specific life-history traits (McGill et al., 2006). One of the most relevant traits regarding the functioning of a community is body mass of individual species (Lawton, 1990; Saint-Germain et al., 2007), as it encompasses many of the species life-history traits (Lewis et al., 2008; Peters, 1983; Peterson et al., 1998): it relates to ecological, physiological and behavioural aspects of animals (Damuth, 1987). One of the metrics to assess the structure of communities that includes variation in this trait is the species density – body mass relationship (hereafter referred to as the DBM relationship) (Peters and Wassenberg, 1983). A negative relationship between species 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, 1987, 1981). When considering several trophic levels, the value b has been reported to be close to −1 (Boudreau and Dickie, 1992; Peters and Wassenberg, 1983; Schmid et al., 2000). However, these exponent values have not always been found, and even positive relations have been observed (Maxwell and Jennings, 2006; e.g., Russo et al., 2003). If the DBM relationship has indeed an exponent $b = -0.75$, and given that the individual metabolic rate increases across body mass with an exponent $b = +0.75$, then it is predicted that population energy use per unit area (the product of density and individual metabolic requirements) is approximately independent of body mass. This prediction is known as the "energetic equivalence rule" (Nee et al., 1991). Although being presented as a null model (Humphries and McCann, 2013; Isaac et al., 2013), it is yet unclear whether this rule is expected to be found across different levels of productivity (Buckley et al., 2008; Loeuille and Loreau, 2006), because of the inefficient transfer of energy between trophic levels (Maxwell and Jennings, 2006; Reuman et al., 2008). Moreover, when a community is subjected to an environmental modification, such as an increase in productivity or a disturbance, its DBM relationship can reflect this modification (Cyr et al., 1997a; Reuman et al., 2009) because of the changes in density and species composition (and hence, changes in body mass distribution) of the community (Leaper and Raffaelli, 1999).

In this study, we tested whether the combination of different productivity levels (due to a stressor to which species are adapted and that determines a gradient of productivity over a large area) and a disturbance affect the structure of animal communities represented by the DBM relationship that may follow one of three hypotheses (Figure 1). (1) Based on the energy limitation hypothesis, which states that the total abundance of organisms within an ecosystem is limited by the available energy (Currie, 1991; Wright, 1983), 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 DBM relationship, but only increasing the Y-intercept. (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 slope of the DBM relationship (Cyr et al., 1997a). (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 DBM relationship. For instance, it has been shown that more nutrients can benefit to species of the highest trophic level (predators) of a community without affecting the species of the intermediary trophic

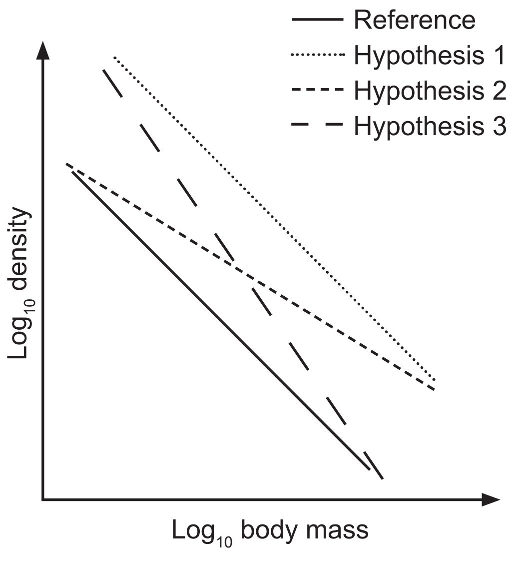

Figure 1: Expected density – body mass (DBM) relationship of the animal communities from sites with different productivity. reference site, i.e., low productivity; expected slope if the total abundance of all the animals increases with increasing productivity, irrespective of their body mass: only the Y-intercept would become higher (hypothesis 1); 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); 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).

levels (Abrams, 1993). Regarding the effect of the disturbance, we hypothesized that it would impede the productivity of the system (Kondoh, 2001), hence disrupting the DBM relationships that would then be shallower (higher value of the coefficient b) than in non-disturbed conditions if the disturbance mostly affects smaller organisms (Cyr et al., 1997a). Conversely, the DBM relationships would be steeper if the disturbance mainly affects the largest animals (Reuman et al., 2009).

Several methods exist to analyse the DBM relationship of a community (Reuman et al., 2008; White et al., 2007). As we were interested in how productivity affects the density of all species and of specific body mass categories, we chose to compare the local size – density relationship (LSDR) and the individual size distribution (ISD). The LSDR shows the representation of the density against body mass of each individual species, whereas the ISD does not consider taxonomy and shows the distribution of individual body masses within a community using body mass categories (Reuman et al., 2008). We compared the two methods with respect to the ability of the resulting DBM relationship to detect differences in the structure of animal communities along a gradient of productivity. As we expected species life-history traits (here represented by body mass) rather than species per se to directly reflect different structures of community, we hypothesized that the ISD would be more capable of reflecting different community structures inherent to their respective environmental properties. Besides, to be able to better understand and interpret the results of the DBM relationships, we also measured the total density, the total body mass and the average body mass per individual of each community along a 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 durations of sea water inundation periods and monitored the response of soil fauna community, which is largely affected by litter biomass (Chen and Wise, 1999; David et al., 1991; Scheu and Schaefer, 1998). Hence, differences in litter biomass were used to represent different levels of productivity. The most frequently inundated areas (closest to the sea) were expected to be less productive for soil fauna than the rarely inundated ones, because the lower productivity caused by the frequent inundation and high salinity would be reflected in the plant litter (Schrama et al., 2012). The disturbance occurred in some areas where there were cattle and also in cattle-free areas. Grazing from cattle is an important disturbance in salt marshes (Bakker, 1985), affecting the habitat of soil organisms (Andresen et al., 1990).

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 x 2 m) based on the differences of basal elevation, which determines the inundation frequency by sea water: daily, weekly, monthly and annually inundation represented low, lower middle, upper middle and high salt marsh zones respectively

(Hacker and Bertness, 1999). Except for the daily-inundated plot that was only ungrazed, the three other plots (weekly, monthly and annually inundated) were divided in grazed and ungrazed plots. The inundation gradient spanned across 1 km, with plots of each inundation frequency about 300 m apart. The distance between grazed and non-grazed plots, which were separated by a fence, was 15 m. In four sub-plots of 50 x 50 cm located in the corners of each plot, we collected soil fauna of three size classes (Decaëns, 2010) representing the most important species groups with regards to abundance: nematodes (microfauna), Collembola (mesofauna) and macrofauna (see Table 1 of Appendix 3 for the complete list of species and morphospecies in the different plots).

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 with a 35x 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 100x and 400x magnification respectively.

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 x 50 cm Perspex boards, of which 20 cm were in the soil, to obtain a better estimate of the species abundance, preventing animals from coming in or out during sampling time. 96 traps (4 traps x 4 sub-plots x 6 plots) were open for seven consecutive days and emptied every 24 hours. The traps of the daily-inundated plot (4 traps x 4 sub-plots x 1 plot) were also open for seven days, but they were checked every 12 hours 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 hours 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 Table 1 of Appendix 3).

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 hours 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 50 x 50 cm plot was measured using a theodolite.

Besides, three biotic environmental factors were measured: vegetation biomass, litter biomass and litter C:N ratio. Above-ground vegetation and soil surface litter were collected by hand in each plot using 50 x 50 cm quadrates adjacent to subplots used for soil fauna capture. These litter and vegetation samples were then dried at 70°C for 48 hours. The dry biomass was weighed and then expressed in $g.m^{-2}$. Litter C and N contents were estimated using a Fisons EA 1108 CHN-O analyser.

Statistical analyses

First, to test for the differences in animal density, total body mass and average body mass depending on inundation frequency and grazing in each sub-plot, we performed ANOVAs with both the inundation frequencies and grazing as fixed factors, followed by a Sidak post-hoc test for the pairwise comparisons between the groups.

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 GLMs, with the animal densities as the dependent variable, the sites as a fixed factor and the body mass as a covariate. When the GLMs detected a significant difference between the three slopes of one sampling, we tested for the differences between the six pairwise comparisons possible using a Sidak post-hoc test. To test for differences between Y-intercepts, we followed the method proposed by Zar (1996). Due to the low sample size, statistics could not be performed on environmental factors.

RESULTS

Environmental variables

As could be expected, plots closer to the sea had lower elevation above sea level and higher salinity (Figure 2.A and 2.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 (Figure 2.C). Litter biomass in the ungrazed plots strongly decreased with increasing inundation frequency and had low values in the grazed plots (Figure 2.D). Both soil and litter C:N ratios (Figure 2.E

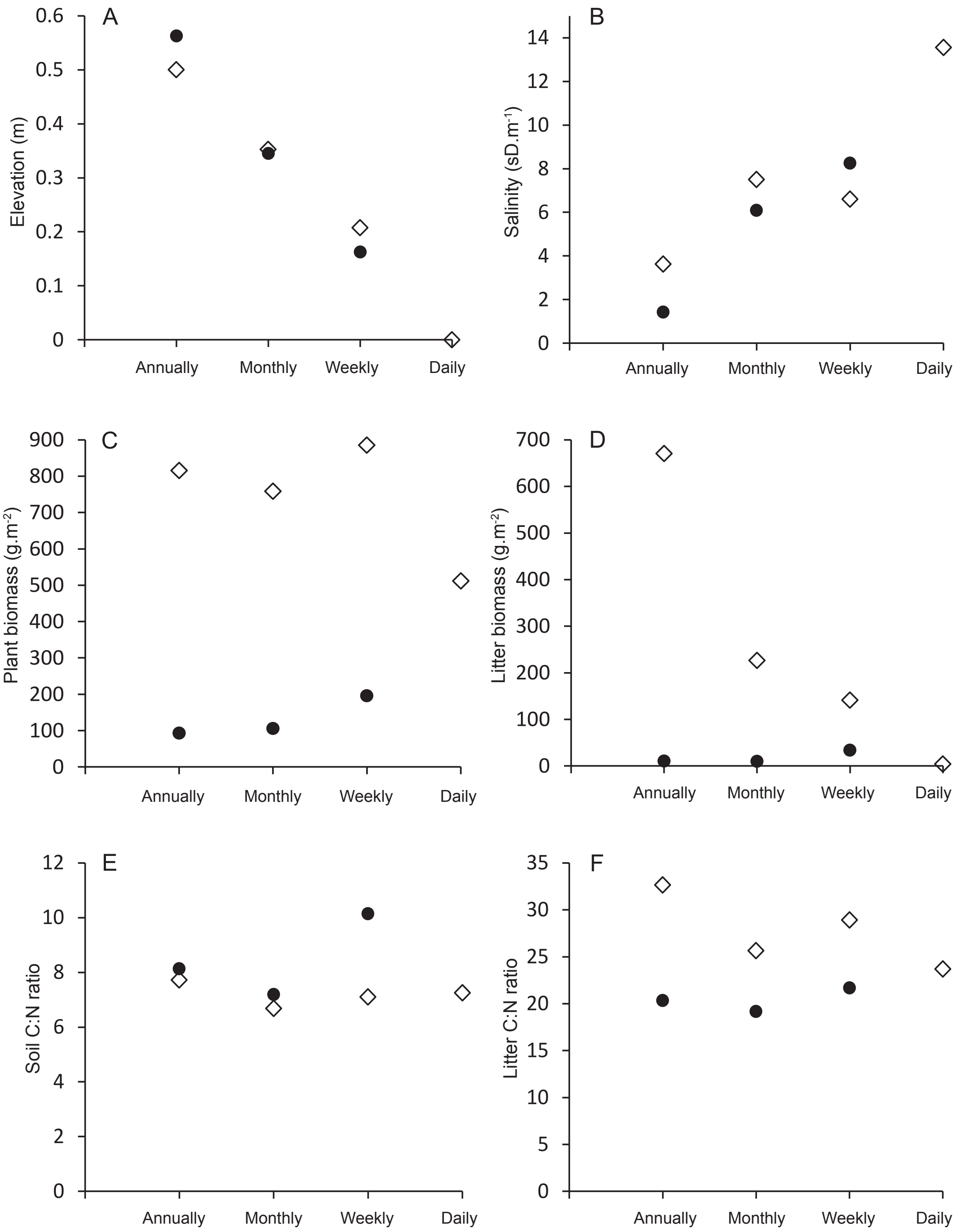

Figure 2: Environmental variables of the grazed (●) and ungrazed (◇) plots depending on their frequency of inundation (annual, monthly, weekly and daily inundation). (A) elevation above sea level using daily inundation as the reference, (B) salinity, (C) plant biomass, (D) litter biomass, (E) soil C:N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

and 2.F) showed no clear change over the inundation gradient or between grazed and ungrazed plots.

Soil fauna responses

The ANOVAs on the total animal density, total body mass and average body mass revealed some differences between the frequencies of inundation, both in the grazed and ungrazed plots (Figure 3 and Table 1). In both the grazed and ungrazed plots, the total density of animals increased as the frequency of inundation decreased (Figure 3.A and 3.B). The total body mass followed a similar pattern in the grazed plots only (Figure 3.B); this pattern was opposite in the ungrazed plots. Likewise, in the ungrazed plots, the average body mass was the highest where the frequency of inundation was the highest (Figure 3.A). In the grazed plots, there was no difference for the average body mass between the different frequencies of inundation (Figure 3.B). The total density of the annually- and monthly-inundated grazed communities was significantly higher than the ungrazed ones (Table 2 and Figure 3). The total body mass 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 did not show any difference between the grazed and the ungrazed plots.

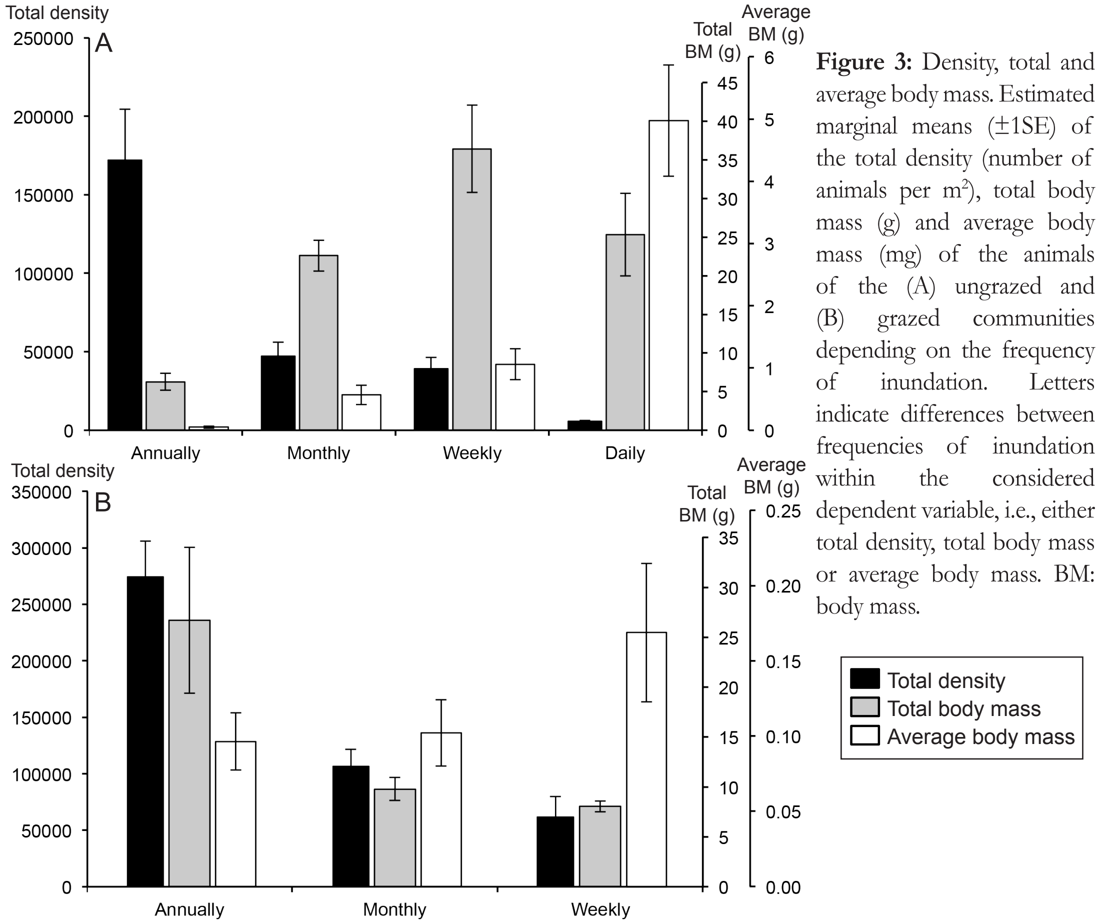

Figure 3: Density, total and average body mass. Estimated marginal means (±1SE) of the total density (number of animals per m^2), total body mass (g) and average body mass (mg) of the animals of the (A) ungrazed and (B) grazed communities depending on the frequency of inundation. Letters indicate differences between frequencies of inundation within the considered dependent variable, i.e., either total density, total body mass or average body mass. BM: body mass.

Table 1: Results of the ANOVAs on the total density, the total body mass and the average body mass in each sub-plot between the frequencies of inundation, in the presence and absence of grazing.

No Grazing			Grazing		
Density	Total body mass	Average body mass	Density	Total body mass	Average body mass
$F_{3,21} = 13.6$ **$P < 0.001$**	$F_{3,21} = 9.0$ **$P = 0.001$**	$F_{3,21} = 39.7$ **$P < 0.001$**	$F_{2,21} = 31.9$ **$P < 0.001$**	$F_{2,21} = 6.2$ **$P = 0.008$**	$F_{2,21} < 0.1$ $P = 0.987$

Table 2: Results of the ANOVAs on the total density, the total body mass and the average body mass in each sub-plot between the presence and absence of grazing, for the different frequencies of inundation.

	Annually inundated	Monthly inundated	Weekly inundated
Total density	$F_{1,21} = 13.2$ **$P = 0.002$**	$F_{1,21} = 4.5$ **$P = 0.047$**	$F_{1,21} = 0.7$ $P = 0.430$
Total body mass (g)	$F_{1,21} = 12.1$ **$P = 0.002$**	$F_{1,21} = 4.8$ **$P = 0.041$**	$F_{1,21} = 23.3$ **$P < 0.001$**
Average body mass (mg)	$F_{1,21} < 0.1$ $P = 0.921$	$F_{1,21} = 0.9$ $P = 0.364$	$F_{1,21} = 3.1$ $P = 0.091$

Table 3: Results of the GLMs comparing the regression slopes between the frequency of inundation of the animal communities for both the local size – density relationship (LSDR) and the individual size distribution (ISD) methods.

		Frequencies	Body mass	Frequencies x BM
LSDR	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	$F_{3,76} = 1.1$ $P = 0.350$	$F_{1,76} = 48.7$ $P < 0.001$	$F_{3,76} = 1.6$ $P = 0.198$
ISD	Grazed	$F_{2,37} = 0.1$ $P = 0.916$	$F_{1,37} = 6.2$ $P = 0.018$	$F_{2,37} = 0.3$ $P = 0.758$
	Ungrazed	$F_{3,53} = 0.2$ $P = 0.910$	$F_{1,53} = 6.3$ $P = 0.015$	$F_{3,53} = 0.2$ $P = 0.930$

The regressions based on the LSDR data showed significant slopes of the DBM relationships for the communities of the grazed and ungrazed plots, except for the daily-inundated one (Figure 4). 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 (Annually inundated: $t_{(47)} = -0.53$, $P = 0.700$; Monthly inundated: $t_{(50)} = -0.95$, $P = 0.828$; Weekly inundated: $t_{(36)} = -0.78$, $P = 0.781$). GLMs 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 3). However, among all the pairwise comparisons between the frequencies of inundation, the annually and

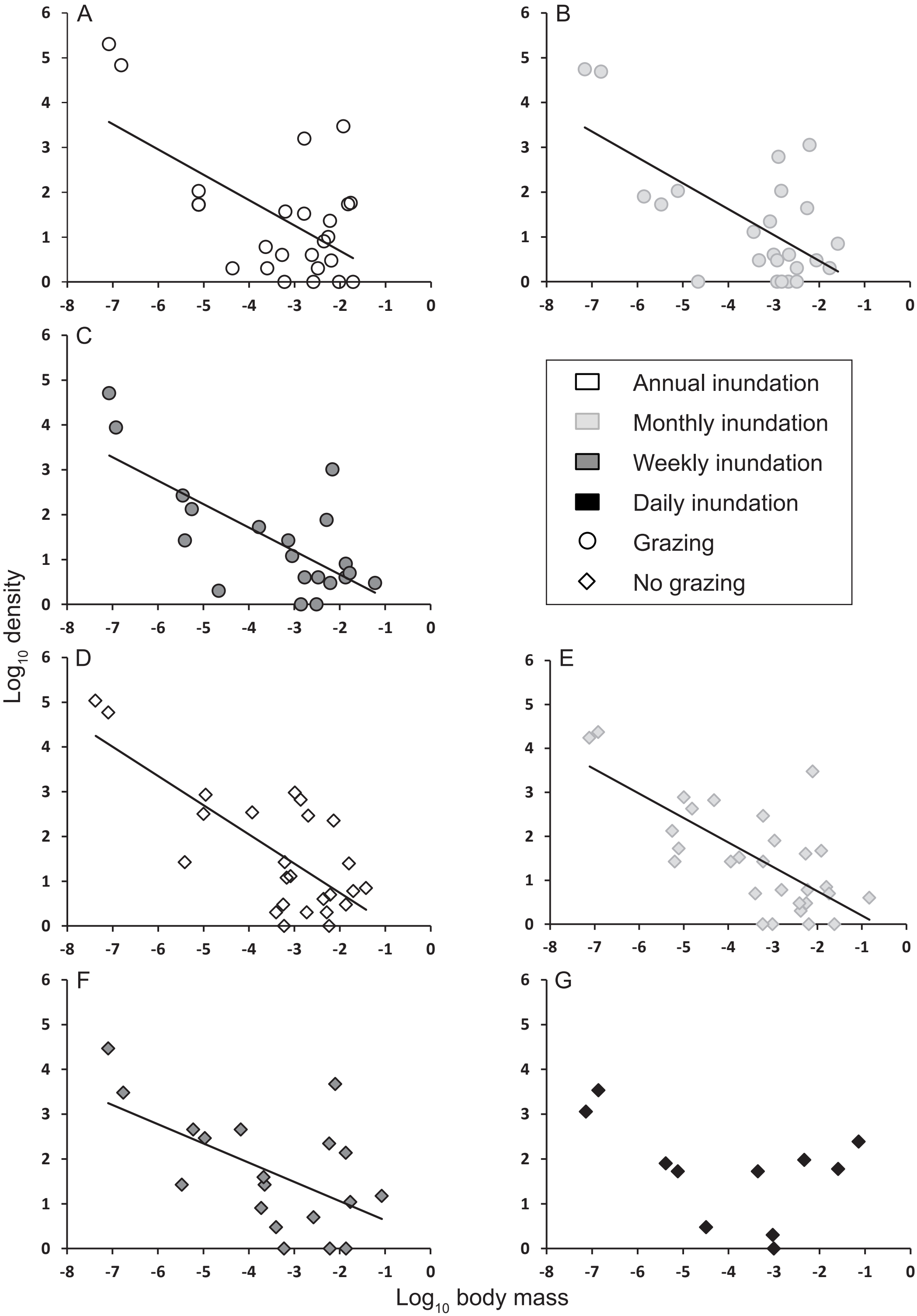

Figure 4: Regressions of the density – body mass relationships based on the local size – density relationship (LSDR) of the grazed and ungrazed plots subject to (A, D) annual, (B, E) monthly, (C, F) weekly or (G) daily inundation. Significant relationships have a trend line. Sl.: slope (±1SE); R^2: adjusted R^2.

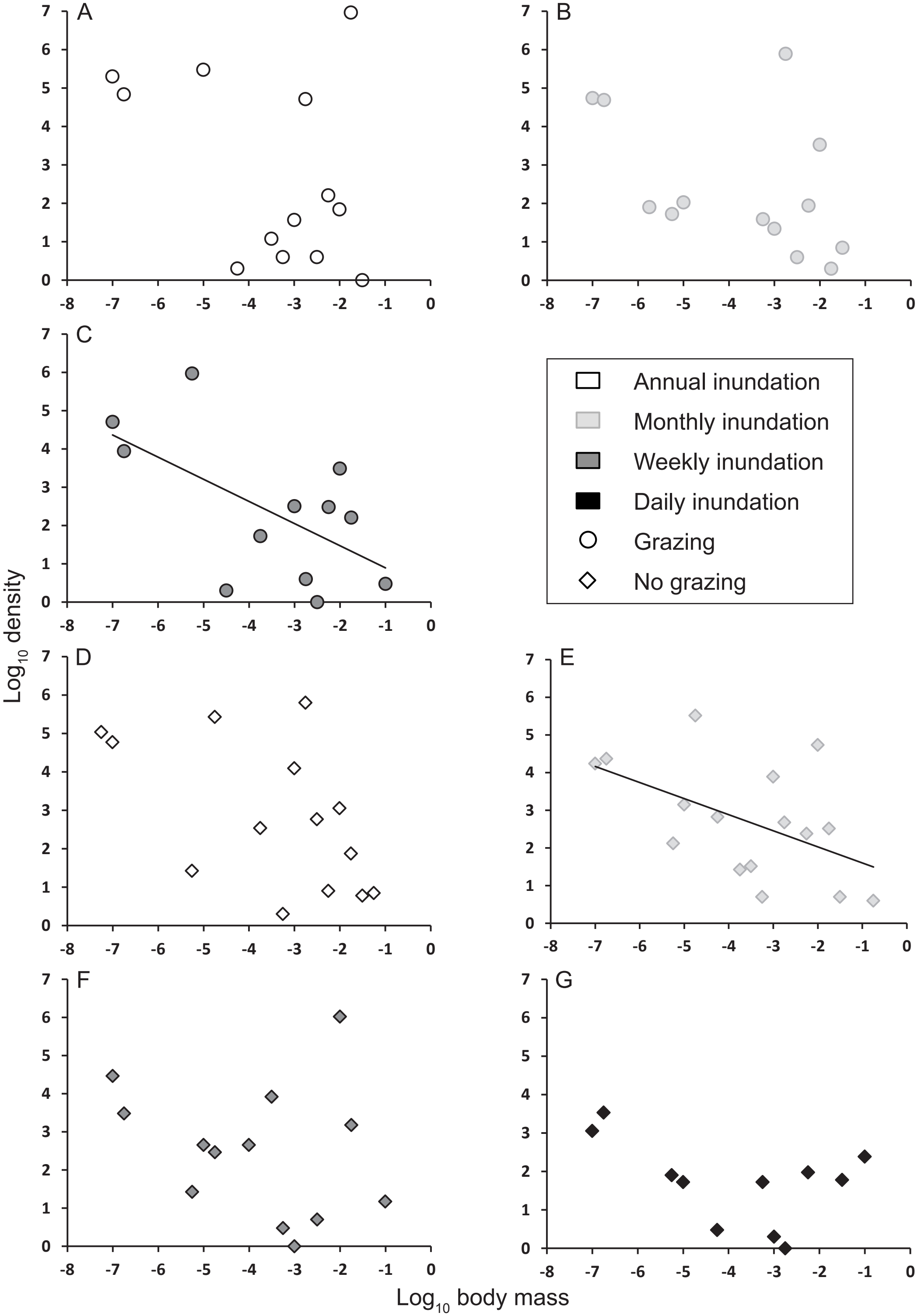

Figure 5: Regressions of the density – body mass relationships based on the individual size distribution (ISD) of the grazed and ungrazed plots subject to (A, D) annual, (B, E) monthly, (C, F) weekly or (G) daily inundation. Significant relationships have a trend line. Sl.: slope (±1SE); R^2: adjusted R^2.

daily inundated ungrazed plots appeared to be significantly different after applying the necessary corrections (i.e., Sidak post-hoc test) (Table 4). The regressions based on the ISD data showed only two significant DBM relationships for the monthly-inundated grazed plot and the weekly inundated ungrazed one (Figure 5). The Y-intercepts did not differ either between the inundation frequencies (Grazed: $F_{2,39} = 0.24$, $P = 0.792$; Ungrazed: $F_{3,57} = 1.92$, $P = 0.137$), nor between the grazed and ungrazed areas (Annually inundated: $t_{(36)} = 0.06$, $P = 0.477$; Monthly inundated: $t_{(26)} = -0.70$, $P = 0.755$; Weekly inundated: $t_{(22)} = -0.04$, $P = 0.517$). None of the ISD-based slopes were significantly different from one another (Table 3 and 4). For both the LSDR and the ISD data, there were no differences between the slope of the DBM relationships of the grazed and the ungrazed plots subjected to the same frequency of inundation (Table 5).

Table 4: Pairwise comparisons of the regression slopes between the frequencies of inundation of the animal communities for both the local size – density relationship (LSDR) and individual size distribution (ISD) methods.

		Annually vs. monthly	Annually vs. weekly	Monthly vs. weekly	Annually vs. daily	Monthly vs. daily	Weekly vs. daily
LSDR	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
ISD	Grazed	*P* = 0.739	*P* = 0.460	*P* = 0.690	N.A.	N.A.	N.A.
	Ungrazed	*P* = 0.707	*P* = 0.758	*P* = 0.544	*P* = 0.837	*P* = 0.609	*P* = 0.930

Table 5: Results of the GLMs comparing the regression slopes on the presence and absence of grazing on the animal communities for both the local size – density relationship (LSDR) and individual size distribution (ISD) methods.

		Grazing	Body mass	Grazing x Body mass
LSDR	Annually inundated	F1,46 < 0.1 P = 0.866	F1,46 = 36.0 P < 0.001	F1,46 = 2 P = 0.672
	Monthly inundated	F1,49 = 0.3 P = 0.612	F1,49 = 41.3 P < 0.001	F1,49 < 0.1 P = 0.894
	Weekly inundated	F1,35 = 0.6 P = 0.443	F1,35 = 24.5 P < 0.001	F1,35 = 0.2 P = 0.630
ISD	Annually inundated	F1,35 < 0.1 P = 0.907	F1,35 = 2.2 P = 0.144	F1,35 < 0.1 P = 0.918
	Monthly inundated	F1,25 = 0.1 P = 0.809	F1,25 = 7.4 P = 0.012	F1,25 < 0.1 P = 0.947
	Weekly inundated	F1,21 = 0.8 P = 0.376	F1,21 = 4.6 P = 0.044	F1,21 = 1.0 P = 0.334

Discussion

In this study, we tested whether the level of productivity of ecosystems affects 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, the DBM relationship is expected to reflect changes in the community's structure due to changes in the level of productivity (Cyr et al., 1997a; Reuman et al., 2009). Results of studies on the DBM relationship have shown much discrepancy in regression slopes or distributions (Brown and Maurer, 1987; Maxwell and Jennings, 2006; Morse et al., 1988; Nee et al., 1991; Russo et al., 2003; Silva and Downing, 1994; Ulrich et al., 2005), if any slope at all (e.g., Gaston and Lawton, 1988). When used to detect environmental modifications due to disturbances, the DBM relationship 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 DBM relationships of soil fauna communities over a productivity gradient (due to sea water inundation frequency) and the presence or absence of a disturbance (grazing). Besides, we used several ecological indices (i.e., the total density, the total body mass and the average body mass) to help characterizing the communities and compared them to the DBM relationships. These indices showed that, in the ungrazed plots, there were many small soil organisms in the less inundated plots and few big animals in the most inundated ones (Figure 3.A). This suggests that, as productivity is the highest in the annually inundated plots, represented by the high quantity of litter biomass in these plots (Figure 2.D), there were more small individuals in the high productivity plots to the expenses of the large ones. This agrees with Cyr et al. (1997a), who found more productive systems 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 based on the LSDR from sites with annual to daily inundation (Figure 4.D – 4.G) (Cyr et al., 1997a; Jennings and Mackinson, 2003). As we sampled a wide range of 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).

The DBM relationships in our study were based on a wide range of body masses (Cyr et al., 1997a, 1997b; Stork and Blackburn, 1993). Although our sample size was relatively low (as regard to the number of plots), we could show an increase of the slope of the DBM relationships for soil fauna communities as function of increasing productivity (represented by litter biomass). Using the LSDR approach, we found slopes varying from –0.43 to –0.65. Given the changes in the DBM relationship with increases in productivity, one can expect that the population energy use per unit area (the product of density and individual metabolic requirements) is not constant over a range of body masses as stated by the energetic equivalence rule (EER) (Nee et al., 1991). By ignoring the exact values of the slope of the DBM relationship in our study, but merely looking at the relative changes, our findings suggest that the population energy use per unit area will decrease as function of body mass along a gradient of productivity. Studies on phytoplankton and plant communities have managed to show that the energetic equivalence rule could correctly predict scaling of numerical abundance and body mass (Belgrano et al., 2002; Li, 2002). Andrew and Hughes (2008), who compared insect communities of different latitudes, did not succeed in finding differences between the DBM relationships of each location. These various results could be explained by the fact that the DBM relationship may be described by different functions (with different values for b in the equation $D = a\cdot M^{b}$) at different trophic levels (Lewis et al., 2008) or between taxa with different physiologies, from one level to another. 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; Marczak et al., 2007; Maxwell and Jennings, 2006). This could suggest that the EER may stand for within-trophic-level comparisons, but fails for between-trophic-level comparisons.

Of the two methods that we used to calculate the DBM relationship (i.e., the LSDR and the ISD), the LSDR allowed to obtain six out of seven significant relationships (Figure 4), whereas only two relationships were significant when using the ISD (Figure 5). Because the ISD method pools together the species according to the body mass category they belong to, the resulting relationships are therefore based on less data points (one per category for the ISD instead of one per species for the LSDR), which may explain the higher P and lower R2 values of the ISD slopes. As research questions involving body mass and energy distribution within communities seldom focus on species, the ISD method is preferable to the LSDR for those studies (Reuman et al., 2008), but the range of body masses should span as many orders of magnitude as possible to obtain sufficient data points to fit the ISD. However, the LSDR is more recommended to understand relative species densities, such as in biological conservation matters (Belgrano et al., 2005).

In our study, we used litter biomass as a proxy for productivity as soil fauna communities are found to increase in species abundance and richness with litter biomass (Barberena-Arias and Aide, 2003; Batzer and Wissinger, 1996; Lavelle, 1996). 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). Another proxy could have been the quantity of 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. It should be noticed that the quality of the litter may also play a role (Batzer and Wissinger, 1996) and that it may differ depending on the frequency of inundation by sea water. Besides, 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). Likewise, grazing may have modified the vegetation height, the soil's exposition to drought, as well as soil composition and compaction (Coffin et al., 1998; Schrama et al., 2012).

Regarding the influence of grazing on the communities, in the ungrazed plots, the animal total body mass 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 disturbance modified the resource availability or use from the soil fauna. We can assume that the combination of both the low productivity and the impacts 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 (i.e., making the DBM slopes shallower).

The DBM relationship is an energetic relationship that can provide information on the 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). We were able to detect differences between similar communities living in environments whose productivity differed, comparable to Cyr et al. (1997a), who studied aquatic systems subjected to a disturbance. Our findings were supported by simple ecological indices such as the total density, total body mass and average body mass, except for the effect of grazing. This study shows that the DBM relationship has the potential to be used in conservation biology and may allow making predictions on its deviation depending on environmental influences over space and time.

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CHAPTER 6

In this last chapter, I combine the findings of the previous chapters to synthesize the contributions of this thesis to the study of the effects of disturbances on the structure of animal communities and to generalise ideas about recovery. The difficulty in apprehending the complex matter of disturbance and recovery in community ecology comes from the fact that it depends on several factors and their interactions. Among these factors, the main ones are the characteristics of the disturbance itself (e.g., duration, intensity, frequency), the characteristics of the environment (e.g., productivity, climate, structure and heterogeneity at various scales) and the characteristics of the community (e.g., species abundance and richness, and traits of individual species). This generates manifold combinations of characteristics that should be acknowledged when developing methods to make predictions on recovery. By testing the effects of different types of disturbances on the recovery of soil and litter fauna communities in environments with different levels of productivity, this thesis contributes to better understanding the main factors influencing the impact of a disturbance on an animal community and its subsequent recovery. I then propose ways to enhance nature conservation by anticipating disturbances and methods to better predict recovery and improve restoration.

Effects of the intensity of the disturbance

Although the disturbing agent used in the experiments described in Chapter 2, 3 and 4 (diesel fuel) proved to be effective on the litter and soil fauna, different doses did not always result in differences in the severity of the disturbance on the communities and in the ensuing structure of the communities (Chapter 2 and 3). Differences between different levels of disturbance were only found when using the density – body mass relationships. Even though the ecological indices used in Chapter 2, 3 and 4 were different, the ability to detect quantitative differences only in Chapter 4 may be due to the use of a broader spectrum of biological indicators including nematodes and Collembola (besides the macrofauna also used in the experiments of Chapter 2 and 3), which may be more sensitive to the disturbance.

This type of hydrocarbon had never been used before in dose-effect studies to create a high-impact disturbance and low doses of this disturbing agent appear to suffice to induce a high severity on exposed soil and litter fauna. Therefore, a disturbance of this nature requires a low quantitative threshold to impact a large portion of litter fauna communities and an n-fold increase in the dose of disturbing agent may not be reflected in an n-fold higher mortality rate.

In the work described in Chapter 5, I used light grazing as a disturbance, which did not seem to have direct lethal consequences for the communities, but nonetheless impacted their structure by promoting the communities (i.e., their density and biomass) in plant-productive areas. This contradicts the results usually found about the impact of light grazing, which stimulates plant species richness (Pykälä 2003) but negatively affects invertebrates (Andresen et al. 1990) because it suppresses plant litter in which these animals live (Andresen et al. 1990; David et al. 1991).

Effects of climate and productivity

In the small-scale experiment of Chapter 5, the effect of grazing on soil and litter fauna communities from low-productivity areas (resulting from frequent inundation and high salinity) created a constraining environment that reduced species richness and abundance, compared to high-productivity areas. Indeed, grazing displaced the communities with the highest density and biomass from the low-productivity areas to the high-productivity areas, which would explain the results described in the previous paragraph as to why grazing promoted the communities in high-productivity areas.

In my thesis, I also investigated the effect of productivity in a large-scale experiment comprising two biomes with different climates (a boreal and a temperate forest). Although the rate of recovery was similar in both biomes (Chapter 1), species assembly differed, as I found that there was less variation in the boreal forest within the same communities from one year to another than in the temperate forest (Chapter 2). Therefore, among-replicate variation may depend on environmental conditions and, in low-productivity environments, the response to disturbance may be less variable. I argue that niche theory could then better explain species assembly in these environments, as this theory considers that deterministic processes (rather than stochastic ones) influence species assembly. The latter is then determined by the adequacy between species life-history traits and the environmental conditions (i.e., environmental filters). Over an altitudinal gradient, Kluge and Kessler (2011) found that constraining environmental conditions filtered species, clustering species with regard to their traits, and Wassenaar et al. (2005), studying the recovery of coastal dunes, found that recovering communities converged toward a similar composition. This supports my findings that niche theory may better explain species assembly mechanisms in more constraining environments. The environmental filters induced by climatic constraints may only influence the structure and composition of the communities, as these constraints did not impede the rate of recovery, which was similar in both biomes.

In his artificial pond experiment, Chase (2010) found that high productivity induced high biodiversity, which then increased the possibility of alternate communities, thence promoting stochasticity in species assembly. Under natural conditions, in a biome exhibiting high productivity and biodiversity such as a tropical rain forest (Gaston and Blackburn 2000; Hillebrand 2004), I would expect such patterns to be found as well, besides a faster recolonization due to the constant high temperatures (increasing the degradability of the diesel fuel and the dispersal capabilities of the fauna) and to the high species richness and abundance.

Effects of the environment

To assess the effects of disturbances and the subsequent recovery, the environment should be considered at several scales. Firstly, at the scale of each study site of Chapter 2, 3 and 4, the surrounding environment served as a species pool for recolonization of the disturbed plots (Holling 1973; Brudvig 2011), as the rapidity of the re-establishment of the communities cannot support the hypothesis of a recolonization from the surviving animals, which have a much longer reproductive cycle (Ribera et al. 1999; Turin 2000). The fact that I did not find a recolonization pattern from the outer samples of the plots toward the inner samples in Chapter 2 and 3 is actually an illustration of the speed at which the surrounding animals have recolonised the disturbed plots. Therefore, if recovery can be determined by the species pool of the surrounding environment (Holl et al. 2003), the connectivity of an ecosystem may be very important for its stability (Brudvig et al. 2009) and recovery should be considered at the landscape scale to be effective (Palmer et al. 1997).

Secondly, at a much smaller scale than a whole study site, the results of Chapter 2 showed that the environmental microstructure, i.e., the structure of the habitat I assumed to be directly perceived by the macrofauna, must have had a dramatic effect on the outcome of the disturbance. Indeed, the leaf litter layer that covered the forest floor in the temperate biome seems to have greatly protected the arthropods from the disturbance, compared to the abundance of the boreal fauna that plummeted just after the disturbance. The temperate macrofauna must have found refuge inside or beneath the thick litter layer (up to 5 cm). The potential protective role of the litter layer from exogenous disturbances does not seem to have been documented. The litter layer is known for protecting the soil's structural integrity (i.e., the soil's pores) upon which the fauna depends (Bridge et al. 1983), for providing a shelter to the fauna by regulating the temperature and moisture (Gill 1969; David et al. 1991) and, in a recent paper, it was shown to protect caterpillars, which could hide in the litter layer, from predating ants (Karban et al. 2013). The results of this thesis suggest that the litter layer can greatly contribute to the resistance of a whole community seeking refuge into it and this environmental element should not be neglected in future cases involving a disturbance in a litter-covered area. Likewise, other elements of the microstructure of the environment, such as holes, stones, bark, puddles, etc. could provide a shelter for some animals and the spatial heterogeneity of the habitat may contain some refuges in the case of certain disturbances.

Effects of the pre-disturbance structure of the community

Communities with high species richness seem to be more resistant than low-richness ones, as the relative species loss of high-species richness communities levelled off at 50%, whereas it was higher for intermediate-richness communities (Chapter 2, Figure 2.C and D). This could be seen as an important loss, but the recovery index used in Chapter 2 showed that species richness was not negatively impacted by the disturbance (Chapter 2, Figure 3.C and D), unlike species abundance and biomass. Moreover, after the disturbance, all the feeding types that had been found prior to the disturbance were still present. This may be due to the relatively high richness illustrating the insurance hypothesis (Naeem 1998; Yachi and Loreau 1999) that allowed the remnant community to still have all the feeding types.

One of the main life-history traits that appeared to be essential for both the resistance and recovery of litter macrofauna was the ability to disperse well. Animals with good dispersal capabilities could, firstly, avoid the disturbance by fleeing from it (Chapter 2, Figure 5.A) and, secondly, after the disturbance, be the first to recolonise the newly available habitat and enhance the recovery of the community.

Regarding the total abundance of the pre-disturbance community, contrary to one of my hypotheses in Chapter 2, it did not enhance the resistance of the community. On the contrary, the higher the total abundance was before the disturbance, the more severe (deleterious) the disturbance was for the community (Chapter 2, Figure 2.A and B). This, combined with the resistance of communities that is enhanced by a high species richness, could provide information on the potential resilience of communities, especially if the recovery mostly depends on the surviving animals as a source for re-establishment (e.g., in the centre of widely disturbed areas, in fragmented landscapes where the disturbed area is not connected to a source community or in the case of bad-disperser communities). While the total abundance of a community can give some hints about its risk of abundance loss in the case of a disturbance, its species richness can inform on its resilience. Therefore, the results of my thesis support the idea that nature conservation plans should focus on increasing species richness rather than abundance as a means of enhancing community resistance and recovery.

Density – body mass relationship

In the two previous chapters of this thesis, I found that the considered communities of soil and litter fauna supported the density – body mass relationship (DBM relationship), even though this relationship is sometimes regarded as controversial, as some studies empirically confirmed it (Damuth 1981; Cyr et al. 1997a, 1997b; Reuman et al. 2009) whilst other did not (Gaston and Lawton 1988; Russo et al. 2003; Maxwell and Jennings 2006; Andrew and Hughes 2008). This discrepancy may be explained by the necessity to sample a broad spectrum of body masses (Lawton 1989; Blackburn et al. 1993; Cyr et al. 1997a; Arneberg and Andersen 2003) (hence combining several sampling methods) and by the fact that there may be different energetic rules for different taxonomic groups and thus, the energetic equivalence rule may only stand for within-trophic comparisons and is not valid anymore when considering several trophic levels. The energetic theory describing the flow of energy within the system, which depends on organisms' body mass and density, may therefore have to be adapted to take into account various trophic levels within a community. Thus, the expected value of the slope, which is currently −0.75, may be found to be theoretically different depending on the number of trophic levels taken into account.

My results in Chapter 4 and 5 show that changes of the DBM relationship could reflect the response of community structure to modifications of the environment, be they disturbances or differences in productivity; the slope of the DBM relationship of communities from disturbed or low-productivity environments seems to be less steep than the slope of communities from high-productivity or undisturbed environments. Using this relationship, I could even detect differences in the structure of communities impacted by different doses of disturbing agent, which the indices that I used in Chapter 2 and 3 did not succeed to achieve; this higher accuracy may be due to the broader range of species collected for the DBM relationship.

I suggest that the DBM relationship could be used as an index to monitor the state of the structure of communities. Thus, in studies limited in time and/or budget, and aiming at assessing the structure of communities, the DBM relationship has the advantage of only requiring collecting organisms, counting them and determining their weight. Attention should however be paid on the range of body masses to sample. This method is less constraining than having to identify the species and then, their life-history traits, which usually requires a lot of time and (costly) expert knowledge. This relatively simple method may be used to probe communities and detect early warning signals of communities about to change state (Scheffer et al. 2001) by comparing the respective characteristics of the relationship (e.g., slope, variance, significance) with former records. Different slopes from previous records may indicate quick variations in the structure of a community (distribution of the body masses), which may reflect a lack of resilience of the community, which could be an early warning signal for a critical transition (Dai et al. 2012; Scheffer et al. 2012). However, the sampling methods required to collect data for the density – body mass relationship are usually invasive, and frequent sampling has to be undertaken to be able to properly assess the variability of the density – body mass relationship (Carpenter et al. 2011) and this sampling alone may be a disturbance.

Recovery

In each of the three chapters of this thesis dealing with recovery (i.e., Chapter 2, 3 and 4), I have used a different tool to measure recovery, even though all three chapters pertained to the same hierarchical level of the ecosystem, the community. This point needs to be highlighted as it illustrates the necessity to use the most appropriate tool to answer the question asked, as recovery can be apprehended through many different indices.

In Chapter 4, I tested the usability of a known index (the DBM relationship) to indicate the state of the structure of a community subjected to a disturbance. The aim of this chapter was to demonstrate the ability of this index to effectively show patterns of recovery of communities, which had never been done before. The high significance of the slopes that I found showed that the DBM relationship can be used as an effective indicator of changing structures of soil and litter fauna communities. The strength of this index in the context of recovery can certainly be attributed to the characteristics that it takes into account, directly and indirectly, i.e., a wide range a organisms and how energy flows within the community (Nee et al. 1991).

In Chapter 3, I chose to use the dissimilarity between species assemblages of communities to assess their recovery. Therefore, I used a common dissimilarity index, the Bray-Curtis index, to compare species assemblages. However, I first checked whether this index would be the most appropriate to answer my specific question, and decided not to apply the Wisconsin double standardisation after I tested its effect on the Bray-Curtis index in a situation comparable to my study. To reach this conclusion, I first simulated situations in which samples to be compared for their dissimilarity were either homogeneous (i.e., within the same range of numbers, therefore, rather similar) or heterogeneous (i.e., within different ranges of numbers, therefore, very dissimilar). When the Wisconsin double standardisation was first applied to the Bray-Curtis index, the capability of the index to detect dissimilarity between heterogeneous samples was much lower than without the standardisation. As the likelihood of having to deal with heterogeneous samples was high in a study focussing on recovery, I chose not to apply this standardisation. Hence, carefulness should be advocated before using existing indices, as it may be necessary to adjust them so that they are properly adapted to a specific question.

Finally, in Chapter 2, as no existent index that I knew of could give indications on the state of recovery of communities based on species richness, abundance and biomass, while considering control communities, I created a simple "recovery index" that fitted my requirements. My aim was to take into account the initial and the current state of the undisturbed communities as a control to compensate for the natural variation of communities (Parker and Wiens 2005; Ives and Carpenter 2007). This index proved very effective and such a simple index must be easy to implement in many other studies, but it requires an essential piece of information to assess the recovery of a system, the initial undisturbed state, which is unfortunately seldom known (Niemi et al. 1990).

Even though each index was used to answer a different question, if I consider the data they take into account, the results they gave, their ease of use and their consistency, I would conclude that the index that proved the best at indicating the state of recovery of communities was the "recovery index" that I created for the analyses of Chapter 2. The main advantages of this index are its usability on several ecological indicators (e.g., species abundance, species richness, biomass, abundance of traits) and the fact that it considers the pre- and post-disturbance states of both the disturbed and control communities (which is its purpose). However, it requires knowing the taxonomy and/or life-history traits of each animal. The DBM relationship does not require such an exhaustive identification and it gave very satisfying results in Chapter 4, but as the relationship was sometimes not significant in Chapter 5, it shows that it may not be easily applicable in every case. Regarding the Bray-Curtis dissimilarity index used in Chapter 3, even though it is designed to compare the structure of entire communities between each other, it cannot take into account the pre- and post-disturbance states of both the disturbed and control communities, and therefore, it does not consider the natural variation of communities.

As shown earlier, species assembly of recovering assemblages is usually explained by either the niche or the neutral theory. Though these two theories have often been opposed (Adler et al. 2007), my hypothesis in Chapter 3 was that both theories were not mutually exclusive and that the degree of importance of each deterministic and stochastic process may depend on the characteristics of the biome (Power 1999). The approach that I chose to determine whether species assembly was indeed more influenced by deterministic or stochastic factors depending on the environmental conditions differed from many other studies, which aimed at trying to find a theory that could fully explain species assembly (Bell 2001; Hubbell 2001; Maurer and McGill 2004). These theories would have most likely failed to find patterns in my study case, as the results of Chapter 3 were not very conclusive for either deterministic or stochastic processes, indicating that species assembly in Chapter 3 indeed depended on both processes.

At the moment, the multiple random factors involved in disturbance and recovery make it very complicated to establish a species assembly theory, but another exogenous deterministic factor increasingly influences the outcome of recovery: the role of human beings. Damaged ecosystems are more and more restored (Dobson 1997; Lake 2001; Holl et al. 2003), hence following a recovery path imposed by humans. As humans may want to influence the recovery of ecosystems (mostly to repair anthropogenic damages), decisions have to be taken about what a recovered community should be composed of (and for what purpose). Different, if not opposite, choices have already been made depending on the aim of recovery, and the future of nature conservation may greatly differ depending on the winning choice. In some cases, the aim is specifically on flagship species (Boates and Fenton 2011) with more or less success (Gratto-Trevor and Abbott 2011; Suding 2011). Many other restoration plans promote ecosystem services to increase the usefulness of nature to humans, for instance by improving carbon sequestration (e.g., Jindal et al. 2008), increasing wood production (e.g., Lynch et al. 2000), enhancing damper zones against disturbances to protect inhabited areas (e.g., Tilley and Brown 1998). As humans seem to want to influence the path of recovery (Gårdmark et al. 2003) and control ecosystems more and more ("and thus render ourselves the lords and possessors of nature" (Descartes 1637)), the process of recovery appears to be in a critical position as it is intertwined with restoration ecology, conservation biology, ethics, societal management and policy. From the results of this thesis, I suggest to take into account more elements of the ecosystem (and their interactions), rather than focussing on a few species or ecosystem services, to help preserve biodiversity, as I have showed that more species favour the resistance of communities, that the path of recovery may be influenced by ecosystem productivity, and that the surrounding areas and microstructure of the environment are key elements for resilience and recovery.

Predictability of recovery

The ability to make predictions is one of the many aims of science (Wilson 1999; Prins and Gordon 2013) and, in the context of recovery, this could be very useful for nature conservation and management (Beisner et al. 2003; Suding et al. 2004), and for restoration (Young 2000; Suding et al. 2004). As it seems that environmental policies have switched from the preservation of existing intact areas to the restoration of damaged areas (Dobson 1997; Young 2000), restoration ecology requires the ability to predict the outcome of a recovery.

Before being able to make predictions on recovery, it should first be known whether some environmental conditions may allow for species assembly to be predictable or not. As I showed in Chapter 3, low-productivity or constraining environmental conditions may favour deterministic processes in influencing species assembly, thence facilitating the predictability of recovery. This may be due to their low richness that does not potentially allow for many alternative stable states (Peterson et al. 1998; Chase 2010). Therefore, in similar areas where species assembly is rather influenced by deterministic processes, recovery will be easily predictable after a disturbance, whereas in areas where stochastic processes overcome deterministic ones, the likelihood of being able to predict the structure and composition of a community after a disturbance will be lower. It would then be worth investigating the processes underlying the mechanism of species assembly (such as the role species traits play in recolonization) in the context of recovery in constraining environments, as these processes will supposedly not be bound by stochasticity in these environments. Consequently, efforts of biological conservation should be considered in a different manner depending on the mechanisms of species assembly in different systems and thus, on the predictability of the recovered communities.

Once it will have been established where predictions are the most likely to be made, the method used to determine the composition of the recovered communities will still have to be chosen. As this thesis shows that many factors (endogenous and exogenous to communities) influence recovery and that stochastic processes play an important role, and knowing that no mechanistic understanding of species assembly exists yet and that restoration ecology only seeks to know the outcome of the processes rather than the processes themselves, the simplest and fastest method for predicting recovery may be a phenomenological approach. By looking at previous empirical studies and observations of the impact that some disturbances (depending on their type, dose, duration, frequency) have had on some communities (whether they are plants or animals and depending on their species richness, abundance, structure) in different environments (type of vegetation, productivity, climatic conditions) and by considering the subsequent recovery (rate, time until completed, species which came back first and their traits), it should be possible to make reliable predictions about the recovery of various situations. This approach would be appropriate for restoration ecology, though it should be stressed that it will not explain recovery and species assembly (Parker and Wiens 2005), but just be coherent with the current understanding.

Characteristics of the biological indicator

This thesis adds some examples of animal communities used to describe species assembly, instead of plants, which are more often used as a model (Gilbert and Lechowicz 2004; Fukami et al. 2005; Grime 2006; Tilman et al. 2006; Adler et al. 2007). The animal group that I chose for my experiments (i.e., soil and litter fauna) have proved to be a good indicator of disturbance and of the ensuing recovery (Rosenberg et al. 1986). This must be due to the fact that the numerous species in this group exhibit various life-history traits (Usher et al. 1982; Koivula et al. 2002; Lindberg and Bengtsson 2006), which are important for ecosystem functioning (Lavelle 1996), and a large range of body masses. Focussing on life-history traits rather than taxa in Chapter 2 allowed me to pinpoint which animal characteristics were impacted, missing or essential in the case of the disturbance and its ensuing recovery. The use of this animal group also gave satisfying results when used to determine density – body mass relationships in changing environmental conditions.

Conclusion

Recovery needs, first, to be precisely defined to assess when and how an ecosystem has reached this state. I propose to use a functional approach that assesses the similarity in trait richness and abundance to measure recovery. Then, the most appropriate tools and indices can be chosen (or created, if necessary) in order to answer specific questions. In this thesis, I adapted a dissimilarity index, created a recovery index, and used the density – body mass index (never used in this context before) to assess the impact of disturbance and recovery of communities from various points of view. While the recovery index proved effective to indicate the state of recovery of communities taking into account relevant information, the DBM relationship appeared to perform well to assess the structure of communities in a changing environment in order to estimate their state of recovery. This thesis shows that the effectiveness and ease of use of these indices may encourage developing their adoption in similar studies.

The combined results of my thesis show that several factors can contribute to better resistance to and recovery from a disturbance; a high species richness and trait richness (among which dispersal capabilities appear essential) rather than high species abundance; a complex and heterogeneous habitat structure that animals can use to find refuge; a species-rich and well-connected surrounding environment, as it may be the main source of colonisers; a high productivity so that, in the case of a disturbance, the environment does not become too constraining and communities can better cope with it.

As disturbances are more frequent and widespread with the expansion of anthropic activities, and nature conservation is shifting from the protection of natural areas to the restoration of damaged ones, predictions on recovery are very relevant to this field. I conclude that the predictability of the outcome of a recovery may be higher in more constraining environments where species assembly is mainly defined by deterministic processes. Therefore, future studies seeking to understand species assembly may focus on such environments before incorporating stochastic processes into their mechanistic models. However, I suggest that managers in charge of environmental conservation use the opposite, phenomenological, approach to rapidly estimate outcomes of recovery and restoration paths, as the mechanistic tools are not available yet.

Finally, as I found that several environmental factors influence recovery, I propose considering more ecosystem elements to elaborate recovery plans than focussing on one species or an ecosystem service, to enhance chances of success and improve the subsequent stability of ecosystems.

Nature unveiling herself before science
(La nature se dévoilant à la science)
Louis-Ernest Barrias

1899. Musée d'Orsay, Paris.
Photo taken by Michel Wal,
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APPENDIX 1 (Chapter 2 and 3)

Table 1: Species collected, their respective abundance in the two biomes at each of the four sampling sessions and their associated life history traits.

	Biome	Temperate				Boreal				Total	Diet*	Body mass (mg)	Dispersal capabilities
	Sampling session	I	II	III	IV	I	II	III	IV				
Carabidae	*Agonum obscurum*	1	7	0	3	7	0	0	1	19	Ca	2.88	2
	Amara brunnea	0	4	0	0	0	0	0	1001	1005	Om	3.91	5
	Amara communis	1	4	0	4	3	11	1	0	24	Om	3.97	5
	Badister lacertosus	1	0	0	1	21	7	0	6	36	—	3.38	2
	Calathus rotundicollis	0	0	0	0	96	377	117	787	1377	Ca	6.11	5
	Calosoma inquisitor	146	1	0	2	0	0	0	0	149	Om	90.61	5
	Carabus coriaceus	0	0	1	0	0	0	0	0	1	Ca	508.50	4
	Carabus glabratus	0	0	0	0	3	3	0	11	17	Ca	238.69	4
	Carabus granulatus	0	1	0	0	0	0	0	0	1	Ca	72.30	5
	Carabus hortensis	0	0	0	0	7	2	0	16	25	Om	193.52	4
	Carabus nemoralis	182	59	6	104	13	4	3	3	374	Om	177.84	4
	Carabus problematicus	0	33	0	0	0	0	0	0	33	Ca	142.19	4
	Cychrus caraboides	0	0	0	0	11	10	0	77	98	Ca	61.40	4
	Dromius agilis	3	0	0	4	1	0	0	0	8	Ca	2.80	5
	Epaphius secalis	0	0	0	0	140	318	0	243	701	—	0.43	3
	Harpalus laevipes	0	0	0	1	3	3	0	8	15	Ca	14.25	5
	Leistus rufomarginatus	2	17	20	1	1	11	13	10	75	Ca	9.32	2
	Limodromus assimilis	2	30	0	67	0	0	0	0	99	Ca	14.90	2
	Loricera pilicornis	3	1	3	2	0	0	0	0	9	Ca	6.02	5
	Nebria brevicollis	22	15	36	106	0	0	0	0	179	Ca	30.72	4
	Notiophilus biguttatus	12	3	0	1	1	0	0	0	17	Ca	2.40	2
	Notiophilus rufipes	92	22	37	71	3	0	6	5	236	Ca	2.40	2
	Patrobus atrorufus	0	0	0	0	2	10	0	25	37	Ca	5.82	2
	Poecilus cupreus	1	0	0	1	0	0	0	0	2	Ca	22.40	5
	Pterostichus aethiops	0	0	0	0	50	3	0	38	91	Om	23.85	3
	Pterostichus melanarius	0	22	0	10	159	29	0	72	292	Om	40.52	4
	Pterostichus niger	3	1	1	0	113	32	0	159	309	Om	62.74	4
	Pterostichus oblongopunctatus	1219	1038	174	2009	49	7	6	22	4524	Om	24.13	3
	Pterostichus strenuus	17	13	3	34	12	12	27	19	137	Om	4.75	5
	Stomis pumicatus	0	0	0	0	4	0	1	0	5	Ca	5.10	3
Geotrupidae	*Anoplotrupes stercorosus*	0	0	0	0	105	153	11	429	698	Ca/Ne/Co/Fu	92.73	5
	Geotrupes stercorarius	0	0	0	0	0	0	0	1	1	Co	435.50	5
	Trypocopris vernalis	0	1	0	5	0	0	0	0	6	Co	104.60	5
	Typhaeus typhoeus	1	0	0	0	0	0	0	0	1	Co	51.50	5
Curculionidae	*Barypeithes araneiformis*	309	256	0	163	0	0	0	0	728	Ph	1.09	3
	Brachysomus echinatus	0	0	0	0	241	79	0	0	320	Ph	0.72	3
	Caenopsis fissirostris	4	18	6	2	0	0	0	0	30	Ph	5.70	3
	Hylobius abietis	0	0	0	0	26	3	0	3	32	Ph	52.11	3
	Hylobius pinastrie	0	0	0	0	34	14	0	71	119	Ph	21.94	3
	Phyllobius argentatus	8	2	0	2	0	0	0	0	12	Ph	2.43	3
	Strophosoma capitatum	75	15	9	22	0	0	0	0	121	Ph	3.22	3
	Strophosoma melanogrammum	23	63	36	320	0	0	0	0	442	Ph	3.22	3
Melolonthidae	*Serica brunnea*	0	0	0	0	0	5	0	43	48	Ph	18.61	5
Silphidae	*Dendroxena quadrimaculata*	23	1	2	8	0	0	0	0	34	Ca	47.60	5
	Nicrophorus vespillo	0	1	0	31	0	17	0	98	147	Ne	55.72	5
	Oiceoptoma thoracicum	0	0	0	0	0	0	0	5	5	Ne/Co/Fu	31.33	5
	Phosphuga atrata	55	9	0	11	149	9	1	11	245	Ca/Ne	30.55	3
	Silpha carinata	0	0	0	0	6	6	0	4	16	Ne	57.18	3
Elateridae	Big	92	11	0	75	16	2	0	3	199	Om	18.91	3
	Medium	102	22	0	114	5	4	0	5	252	Om	4.34	2

	Small	5	11	0	93	0	0	0	0	109	Om	0.81	2
Isopods	*Oniscus asellus*	707	542	422	538	0	0	0	0	2209	Sa	17.76	2
	Philoscia muscorum	3605	4566	130	10757	0	1	0	0	19059	Sa	4.99	2
	Porcellio scaber	205	131	77	203	0	0	0	0	616	Sa	12.55	2
	Trachelipus rathkii	0	0	0	0	43	25	4	34	106	Sa	12.45	2
	Trichoniscus pusillus	35	7	0	22	3	3	0	5	75	Sa	0.31	1
Centipedes	*Brachygeophilus truncorum*	3	13	7	6	0	0	0	0	29	Ca	1.46	2
	Lithobius forficatus	147	263	75	103	57	27	36	44	752	Ca	11.73	3
	Schendyla nemorensis	6	1	0	0	0	0	0	0	7	Ca	9.87	2
Millipedes	*Craspedosoma rawlinsi*	1	0	1	0	0	0	1	0	3	Sa/Co	4.34	2
	Cylindroilulus punctatus	18	24	0	14	5	0	0	0	61	Sa/Co	10.33	2
	Julus scandinavus	109	70	53	136	62	4	5	36	475	Sa/Co	31.45	2
	Mycogona germanica	0	0	0	0	697	621	37	115	1470	Sa/Co	3.77	1
	Ommatoiulus sabulosus	0	0	0	0	288	221	4	169	682	Sa/Co	20.43	2
	Polydesmus sp.	208	228	42	171	988	322	23	241	2223	Sa/Co	17.52	2
	Proteroiulus fuscus	2	10	1	0	10	6	17	3	49	Sa/Co	4.05	2
Formicidae	Wood ant	0	0	0	0	65244	9924	320	51834	127322	Om	1.66	4
	Myrmica spp.	565	2276	78	629	4052	2425	194	2563	12782	Om	0.95	3
Staphylinidae	Large black	149	15	10	23	108	18	3	18	344	Ca	16.38	5
	Medium black	251	321	100	364	182	49	77	65	1409	—	1.59	5
	Small black	151	206	565	109	1743	768	749	2014	6305	—	0.70	4
	Small brown	166	4	346	0	17	0	147	0	680	—	0.41	4
Crytophagidae	Crytophagidae	56	44	19	38	8	5	5	2	177	Fu/ Sa	0.58	3
Catopidae	Catopidae	43	40	137	72	85	276	76	487	1216	Ne/Co	0.97	5
Forficulidae	*Forficula auricularia*	59	75	53	202	0	0	0	0	389	Om	17.85	5
	TOTAL	8890	10517	2450	16654	74873	15826	1884	60806	191900			
	Richness	47	48	30	45	46	42	26	44	75			

*Diets: Ca: carnivore, Co : coprophage, Fu : fungivore, Ne : necrophage, Ph: phytophage, Om: Omnivore, Sa : saprophage, —: unknown

Identification keys used:

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APPENDIX 1 (Chapter 2)

Table 2: Independent-samples t-tests on the total species abundance, richness and biomass of the inner and the outer sampling rings of the three treatments in the temperate and the boreal forest (significant values are bolded).

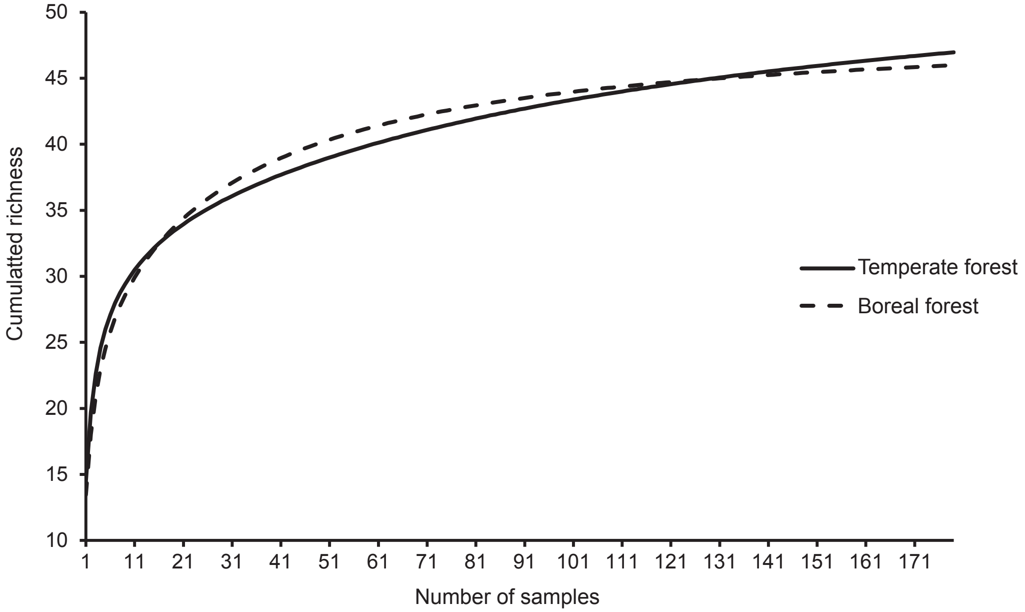
		Abundance						Richness						Biomass					
		Control		Light		Intense		Control		Light		Intense		Control		Light		Intense	
Biome	Sampling	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
Temperate forest	I	1.263	0.266	1.752	0.191	0.047	0.830	0.722	0.393	0.001	0.969	0.327	0.570	0.083	0.775	0.766	0.385	1.557	0.217
	II	1.062	0.307	0.579	0.450	0.099	0.754	5.221	**0.026**	0.198	0.658	2.453	0.123	0.007	0.934	0.025	0.875	1.023	0.316
	III	1.098	0.299	0.318	0.575	0.987	0.325	0.122	0.728	3.050	0.086	0.002	0.966	0.306	0.582	0.827	0.367	1.101	0.298
	IV	4.534	**0.037**	0.004	0.948	2.918	0.093	3.155	0.081	1.717	0.195	0.014	0.916	4.747	0.033	0.034	0.855	2.018	0.161
Boreal forest	I	3.962	0.051	0.354	0.554	0.004	0.949	1.011	0.319	1.200	0.278	0.075	0.785	4.615	**0.036**	0.715	0.401	0.001	0.973
	II	4.087	**0.048**	3.120	0.083	0.080	0.779	0.388	0.536	2.232	0.141	0.441	0.509	1.637	0.206	2.684	0.107	0.295	0.589
	III	0.602	0.441	0.654	0.422	0.063	0.802	0.722	0.399	0.276	0.601	1.191	0.280	3.153	0.081	0.003	0.906	0.001	0.987
	IV	0.495	0.485	0.005	0.947	2.599	0.112	0.558	0.458	0.002	0.964	0.016	0.900	0.806	0.373	0.003	0.955	3.259	0.076

Table 3: Independent-samples t-tests on the recovery indices for abundance, richness and biomass each based on 60 samples (59 degrees of freedom) of the light and intense disturbed plots in the temperate and the boreal forest (values significantly different from zero are bolded).

		Abundance				Richness				Biomass			
		Light		Intense		Light		Intense		Light		Intense	
Biome	Sampling	t	*P*	t	*P*	t	*P*	t	*P*	t	*P*	t	*P*
Temperate forest	II	3.05	**0.003**	5.29	**<0.001**	4.78	**<0.001**	3.62	**0.001**	2.27	**0.027**	1.91	0.061
	III	3.17	**0.002**	2.74	**0.008**	-0.14	0.893	-0.26	0.795	0.42	0.679	1.06	0.292
	IV	1.19	0.240	1.82	0.075	1.49	0.142	1.84	0.071	0.69	0.491	0.18	0.854
Boreal forest	II	-2.29	**0.026**	-2.40	**0.020**	-0.32	0.751	-1.27	0.208	-3.96	**<0.001**	-3.81	**<0.001**
	III	4.41	**0.019**	2.54	**0.014**	4.86	**<0.001**	1.92	0.060	3.10	**0.003**	2.96	**0.004**
	IV	-1.32	0.191	1.90	0.061	2.27	**0.027**	1.35	0.182	-0.265	0.792	1.94	0.058

APPENDIX 1 (Chapter 2)

Figure 1: Species – sampling effort curves of the cumulative samples obtained at Sampling I in the temperate and the boreal forests.



APPENDIX 2 (Chapter 4)

Table 1: Top part: densities of animals according to their body mass class for each sampling and treatment. Bottom part: log-transformed values (log10) of the densities and their corresponding log-transformed (log10) body mass classes. Numbers have been rounded to the second decimal in both tables, but analyses were performed on raw numbers. The animals caught included Araneae, Blattodea, Chilopoda, Coleoptera, Diplopoda, Formicidae, Hemiptera, Mantodea, Oniscidea, Orthoptera, Phasmatodea, Scorpiones and Solpugida.

		Nematodes	Collembola	Pitfall trap arthropods													
Sampling	Treatment	0.18µg to 0.32µg	57.5µg to 100µg	1mg to 1.78mg	1.79mg to 3.16mg	3.17mg to 5.62mg	5.63mg to 10mg	10.1mg to 17.8mg	17.9mg to 31.6mg	31.7mg to 56.2mg	56.3mg to 99.9mg	0.1g to 0.18g	0.19g to 0.32g	0.33g to 0.56g	0.57g to 1g	1.01 to 1.78g	1.79g to 3.16g
I	Control	521000	440	4.03	0.76	-	0.56	0.17	0.10	0.11	0.14	0.41	0.10	-	-	0.10	0.04
	Light	487167	412	2.92	0.23	-	0.48	0.14	0.10	0.14	0.16	0.52	0.11	-	0.02	0.10	0.01
	Intense	493167	388	5.58	2.02	-	1.98	0.08	0.18	0.23	0.12	0.54	0.19	-	0.03	0.14	0.01
II	Control	530000	431	4.46	2.22	-	1.47	0.44	0.32	0.23	0.10	0.22	0.11	-	0.02	0.03	0.02
	Light	175833	213	1.77	3.02	-	0.94	0.40	0.23	0.36	0.11	0.31	0.18	-	0.06	0.02	0.06
	Intense	3600	3	1.74	2.24	-	0.88	0.31	0.20	0.12	0.09	0.13	0.07	-	0.07	0.01	0.01
III	Control	537800	492	2.23	1.34	-	0.78	0.24	0.17	0.16	0.14	0.08	0.26	-	0.03	0.02	0.01
	Light	58258	156	1.49	1.99	-	0.68	0.31	0.27	0.23	0.27	0.13	0.10	-	0.10	0.32	0.04
	Intense	3500	8	1.54	1.19	-	0.66	0.32	0.24	0.42	0.16	0.04	0.16	-	-	0.02	0.14
IV	Control	380667	497	1.46	0.92	-	0.26	0.27	0.08	0.18	0.11	0.21	0.30	-	0.04	-	0.03
	Light	50285	166	1.23	0.91	-	0.37	0.08	0.04	0.12	0.03	0.14	0.18	-	0.09	-	0.07
	Intense	9200	99	1.47	0.81	-	0.44	0.16	0.02	0.21	0.10	0.37	0.08	-	0.14	0.07	0.02

Sampling	Treatment	-6.74 to -6.5	-4.24 to -4	-3 to -2.75	-2.74 to -2.5	-2.49 to -2.25	-2.24 to -2	-1.99 to -1.75	-1.74 to -1.5	-1.49 to -1.25	-1.24 to -1	-0.99 to -0.75	-0.74 to -0.5	-0.49 to -0.25	-0.24 to 0	-0.01 to 0.25	-0.26 to 0.5
I	Control	5.72	2.64	0.61	-0.12	-	-0.26	-0.78	-1.00	-0.95	-0.84	-0.39	-1.00	-	-	-1.00	-1.35
	Light	5.69	2.61	0.47	-0.63	-	-0.32	-0.84	-1.00	-0.84	-0.81	-0.28	-0.95	-	-1.65	-1.00	-1.95
	Intense	5.69	2.59	0.75	0.31	-	0.30	-1.11	-0.75	-0.63	-0.91	-0.26	-0.72	-	-1.48	-0.84	-1.95
II	Control	5.72	2.63	0.65	0.35	-	0.17	-0.35	-0.49	-0.63	-1.00	-0.65	-0.95	-	-1.65	-1.48	-1.65
	Light	5.25	2.33	0.25	0.48	-	-0.02	-0.40	-0.63	-0.45	-0.95	-0.51	-0.75	-	-1.26	-1.65	-1.26
	Intense	3.56	0.48	0.24	0.35	-	-0.06	-0.51	-0.70	-0.91	-1.05	-0.88	-1.18	-	-1.18	-1.95	-1.95
III	Control	5.73	2.69	0.35	0.13	-	-0.11	-0.61	-0.78	-0.81	-0.84	-1.11	-0.59	-	-1.48	-1.65	-1.95
	Light	4.77	2.19	0.17	0.30	-	-0.17	-0.51	-0.57	-0.63	-0.57	-0.88	-1.00	-	-1.00	-0.49	-1.35
	Intense	3.54	0.90	0.19	0.08	-	-0.18	-0.49	-0.61	-0.37	-0.81	-1.35	-0.81	-	-	-1.65	-0.84
IV	Control	5.58	2.70	0.16	-0.04	-	-0.59	-0.57	-1.11	-0.75	-0.95	-0.68	-0.52	-	-1.35	-	-1.48
	Light	4.70	2.22	0.09	-0.04	-	-0.44	-1.11	-1.35	-0.91	-1.48	-0.84	-0.75	-	-1.05	-	-1.18
	Intense	3.96	2.00	0.17	-0.09	-	-0.35	-0.81	-1.65	-0.68	-1.00	-0.44	-1.11	-	-0.84	-1.18	-1.65

APPENDIX 2 (Chapter 4)

Table 2: Results of the RMA. Slopes, SE and R^2 (based on a sampling area for pitfall trap arthropods of $9m^2$).

Sampling	Treatment	Slope	SE	R^2
I	Control	-1.06	0.11	0.88
	Light Disturbance	-1.07	0.11	0.87
	Intense Disturbance	-1.06	0.10	0.90
II	Control	-1.06	0.06	0.96
	Light Disturbance	-0.96	0.07	0.93
	Intense Disturbance	-0.74	0.05	0.95
III	Control	-1.08	0.08	0.93
	Light Disturbance	-0.85	0.08	0.89
	Intense Disturbance	-0.70	0.06	0.91
IV	Control	-1.06	0.11	0.88
	Light Disturbance	-0.95	0.11	0.85
	Intense Disturbance	-0.80	0.09	0.86

Table 3: Results of the GLMs on the densities of arthropods. DBM relationships were computed using the same total abundances of arthropods and considering sampling areas of $6m^2$, $9m^2$ and 12 m^2 (and the same densities of nematodes and Collembola in each of the three cases). The results show that for all the treatments and all the sampling moments, there are no differences between the DBM relationships whether a sampling area of $6m^2$, $9m^2$ or 12 m^2 is considered for the arthropods.

Sampling	Factor	Control	Light	Intense
I	Density	0.698	0.677	0.594
	Body Mass	< 0.001	< 0.001	< 0.001
	Density × Body Mass	0.952	0.954	0.938
II	Density	0.325	0.405	0.162
	Body Mass	< 0.001	< 0.001	< 0.001
	Density × Body Mass	0.870	0.894	0.795
III	Density	0.476	0.494	0.332
	Body Mass	< 0.001	< 0.001	< 0.001
	Density × Body Mass	0.913	0.917	0.858
IV	Density	0.677	0.681	0.523
	Body Mass	< 0.001	< 0.001	< 0.001
	Density × Body Mass	0.947	0.948	0.924

APPENDIX 3 (Chapter 5)

Table 1: of all the species and morphospecies collected in the seven plots, ordered according to their average dry body mass and their total density (in number of individuals per m^2) in the different plots depending on the inundation frequency and the presence or absence of grazing.

		Total density (ind.m^{-2})						
	Body mass	Annually inundated		Monthly inundated		Weekly inundated		Daily inundated
Species or morphospecies	(mg)	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Ungrazed
Nematoda 1	7.30E-05	200182	108811	54974	17440	50804	29193	1137
Nematoda 2	1.36E-04	68244	59145	48529	23506	8720	3033	3412
Parisotoma notabilis	6.37E-03	0	0	0	27	0	0	0
Friesea truncata	6.46E-03	0	318	53	133	133	27	0
Mesophorura macrochaeta	6.59E-03	0	849	80	770	265	451	80
Folsomia agrilla	7.82E-03	53	0	0	0	0	0	0
Archistoma interstitalis	9.77E-03	0	0	0	53	0	292	53
Folsomia sexoculata	1.09E-02	106	0	106	425	27	0	0
Halisotoma maritima	4.69E-02	53	27	0	663	0	451	0
Lepidocyrtus cyaneus	0.12	0	345	0	0	0	0	0
Thalassaphorura debilis	0.12	2	0	1	33	2	39	3
Musca spp. 1	0.27	6	3	0	0	0	0	0
Cantharidae (larvae)	0.37	58	7	7	1	4	1	0
Philoscia muscorum	0.42	3	4	3	3	0	0	0
Entomobrya nicoletti	0.62	0	27	0	27	0	0	0
Araneae 2	0.77	4	12	22	6	12	3	1
Dicheirotrichus gustavii	0.8	0	0	44	6	76	221	0
Pseudosinella alba	0.85	0	955	0	27	0	0	0
Cercopidae spp.	1.3	1	0	1	0	4	0	2
Isotoma riparia	1.5	1566	663	610	292	0	27	53
Carabidae (larvae)	1.56	34	6	3	5	6	12	0
Musca spp. 2	3.25	1	0	1	0	1	1	0
Araneae 1	3.9	4	2	0	40	4	5	0
Hemiptera spp.	4.72	2	2	3	1	0	0	0
Myrmica spp.	4.94	37	13	4	1	0	0	0
Notiophilus spp.	5.65	8	1	0	0	0	0	0
Carcinus maenas	5.88	0	0	0	4	3	15	243
Miridae spp.	6.5	0	0	0	1	0	0	0
Orchestia gammarellus	6.72	23	226	1120	2988	1020	4727	95
Isotoma anglicana	7.39	2946	292	106	80	27	0	0
Cylindroiulus latestriatus	9.5	1	0	0	0	0	0	0
Ovatella spp. 2	13.27	0	0	0	0	0	0	60
Ovatella spp. 1	15.74	0	3	0	47	8	137	0
Chrysomelidae	22.94	54	27	3	9	0	0	0
Staphylinidae	25.9	12	5	7	3	4	1	0
Ochthebius marinus	94.88	0	0	13	5	53	8	0

Taxonomic authorities used for species determination:

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ENGLISH SUMMARY

Disturbances play a great role in ecosystem functioning and, with the increasing anthropogenic activities, they have more and more influence on ecosystems. They have been studied for several decades but recovery, the ecological phenomenon following a disturbance, has seldom been the focus of research. In this thesis, I studied the impact of disturbances on the structure of soil and litter fauna communities and their ensuing recovery in varying environmental conditions, combined with the effect of productivity, life-history traits and community structure. I combined all the results to draw some conclusions on the main factors involved in recovery, how to improve recovery of ecosystems and how to make better predictions on recovery.

In the second chapter of this thesis, I studied how the structure of soil and litter fauna communities from two climatically contrasting biomes was affected by a similar disturbance and how these communities recovered. I sampled litter macrofauna in a temperate and a boreal forest and, to be able to determine whether the communities had recovered, I created a "recovery index" that took into account the pre- and post-disturbance conditions of the disturbed and the control communities, taking into account natural variations. I hypothesised that the temperate communities would recover more rapidly due to the warmer temperatures and to higher species richness and abundance. Recovery was as fast in both biomes, which also had similar species richness. Contrary to my assumption, higher pre-disturbance species abundance did not favour the resistance of communities to the disturbance; on the contrary, high-abundance communities suffered a proportionally greater loss than other communities. Analyses based on life-history traits revealed that dispersal capabilities were the most relevant traits for species facing a disturbance and also for re-establishing. An unexpected factor that influenced the outcome of the disturbance was the litter layer, which, thick in the temperate forest and almost inexistent in the boreal one, protected the fauna of this former biome.

The aim of my third chapter was to consider the main two theories of species assembly, the niche and neutral theory, in the context of a recovery. I considered these two theories not as mutually exclusive but as if they were at opposite ends of a stochasticity gradient. The neutral theory predicts recovered communities in a similar environment to be dissimilar from one another and the niche theory predicts the opposite, because, in this case, species assembly is driven by deterministic factors inherent to communities and to the environment. I used the same experiments as in the previous chapters and hypothesised that the more constraining environmental conditions of the boreal forest would lead to a species assembly rather driven by deterministic factors, with recovered communities more similar to each other than the temperate ones. These latter ones, from a less constraining environment, would be more dissimilar to each other. I found that the structure of each community before and one year after the disturbance was indeed more similar in the boreal forest. This would mean that, in low-productivity environments, the response of communities being less variable, it could be more easily predictable.

In Chapter 4, I studied the structure of communities from a different perspective, using the density – body mass (DBM) relationship to detect changes in the structure of communities after a disturbance. I hypothesised that the slope of the relationship would be less steep if smaller organisms were mainly impacted or that it would be steeper if larger organisms were mainly impacted. By collecting the soil and litter fauna before, just after and again one and two months after a disturbance, I could establish that the DBM relationship reflected the changes of the structure of communities responding to modifications of the environment. In disturbed conditions, the slope of the DBM relationship of a community was less steep, because mainly the small organisms were impacted by the disturbance. I also showed that, at the very early stage of the recovery, the slope was even less steep, because of the large body mass of the first colonisers. This study confirmed the necessity to sample a broad spectrum of body masses and it was the first time that the DBM relationship was shown to be able to reflect changes of the structure of communities. I concluded by suggesting that it could be used for environmental biomonitoring.

After the satisfying results of Chapter 4, I decided to test the ability of the DBM relationship to reflect different structures of communities living in environments varying by their productivity and subjected or not to a disturbance. I hypothesised that communities from low-productivity areas would have a less steep slope than high-productivity area communities and that disturbed communities would also have a less steep slope. To test this, soil and litter fauna were collected from a salt marsh at four elevation levels (hence subjected to varying sea inundation frequencies, from daily to annually), half of which were subjected to cattle grazing (i.e., the disturbance). I assumed that the least inundated sites were more productive and used the quantity of plant litter to confirm this. The only significant result was between the daily and annually inundated ungrazed areas, confirming that communities from high-productivity areas have a steeper DBM relationship slope. High productivity does not seem to equally affect all the trophic levels, certainly due to inefficient transfers of energy from one level to the other.

In the synthesis, I suggested that recovery should first be properly defined to establish when a community has reached that stage and I advise to use pre- and post-disturbance states of control communities for that purpose. Besides, several environmental factors have to be taken into account instead of only focusing on one species or one ecosystem service, as I have showed that the species richness and abundance of communities, and the productivity and heterogeneity of the environment can influence the resistance and recovery of ecosystems. I also propose, in a first time, to study species assembly in constraining environments, where stochastic factors are limited, in order to obtain a better mechanistic understanding of the processes involved. As there is yet not such understanding, I suggest that managers in charge of environmental conservation rather use a phenomenological approach to quickly estimate outcomes of recovery.

Samenvatting

Ecologische verstoringen beïnvloeden het functioneren van ecosystemen. Deze invloed is van groter belang geworden nu antropogene activiteiten toenemen. Alhoewel ecologische verstoringen al decennialang worden bestudeerd, geldt dit in veel mindere mate voor het ecologische proces dat volgt op een verstoring. In dit promotieonderzoek heb ik bestudeerd welke invloed verstoringen uitoefenen op de structuur van bodemfaunagemeenschappen, en hoe het daaropvolgende herstel verloopt gegeven een verscheidenheid aan (omgeving)factoren, waaronder factoren als productiviteit, de initiële structuur van de faunagemeenschap, en levenscycluskenmerken van de bestudeerde organismen. Door alle resultaten samen te voegen ben ik tot een aantal conclusies gekomen over welke factoren het meeste invloed uitoefenen op het ecologisch herstel volgend op een verstoring, en daarmee hoe dit ecologisch herstelproces zowel kan worden voorspeld als gefaciliteerd.

In het tweede hoofdstuk van dit proefschrift beschrijf ik een onderzoek naar de invloed van dezelfde verstoring (en het daaropvolgende herstelproces) op de structuur van twee verschillende bodemfaunagemeenschappen, afkomstig van twee contrasterende klimaatzones. Ik verzamelde samples van macrofauna uit de strooisellaag van enerzijds een gematigd en anderzijds een boreaal bos. Als maat voor ecologisch herstel creëerde ik een ‘herstelindex’. De berekening van dit indexgetal was zowel gebaseerd op de pre- en postverstoringscondities van de verstoorde en controlegemeenschappen, als op natuurlijke variaties. Mijn hypothese luidde dat de faunagemeenschappen van het gematigde bos sneller zouden herstellen dan die van het boreaal bos, als gevolg van zowel de hogere temperaturen als van de hogere soortenrijkdom en –abundantie. In werkelijkheid bleek het herstel in beide biomen even snel te verlopen, en was er bovendien helemaal geen sprake van een verschil in soortenrijkdom. Er was wel een verschil in soortenabundantie tussen beide biomen, maar, tegenovergesteld aan mijn verwachtingen, bleek dat een hogere (pre-verstoring) soortenabundantie niet gepaard ging met een verhoogde resistentie van gemeenschappen tegen verstoringen. Integendeel zelfs: gemeenschappen met een hogere soortenabundantie verloren een evenredig groter deel dan de overige gemeenschappen. Analyses waarin levenscycluskenmerken als verklarende factoren fungeerden, toonden aan dat zowel voor het weerstaan van een ecologische verstoring als voor rekolonisatie, organismen het meeste baat hebben bij dispersiecapaciteiten. Een onvoorziene uitkomst van het onderzoek was dat kenmerken van de strooisellaag zelf ook invloed uitoefenden op de gevolgen van de verstoring. De strooisellaag in de gematigde bossen was veel dikker dan in boreale bossen, en leverde op die manier een betere bescherming op.

In hoofdstuk drie beschrijf ik hoe ik hetzelfde experiment heb aangewend om de twee voornaamste theorieën over soortensamenstelling, de nichetheorie en de neutrale theorie, te beschouwen in de context van ecologisch herstel. Mijn invalshoek was dat beide theorieën elkaar niet uitsluiten maar de extremen vormen van een kansverdeling. De neutrale theorie voorspelt dat gemeenschappen die voorkomen in dezelfde omgeving na een verstoring en het daaropvolgend herstel van elkaar zullen verschillen. De nichetheorie voorspelt het tegenovergestelde, aangezien volgens deze theorie soortensamenstelling de uitkomst vormt van een deterministisch proces waarin omgevingskenmerken en kenmerken van de gemeenschap de verklarende factoren zijn. Mijn hypothese was dat de meer limiterende omgevingskenmerken van boreale bossen (in vergelijking tot gematigde bossen) zouden leiden tot deterministisch bepaalde soortensamenstellingen, waarbij de postverstoring-gemeenschappen meer overkomsten zouden vertonen met de pre-verstoringgemeenschappen, dan in de gematigde bossen het geval zou zijn. Met andere woorden: ik verwachtte dat op boreale bossen de nichetheorie van toepassing was, en dat op gematigde bossen de neutrale theorie van toepassing zou zijn. Inderdaad vond ik dat de structuur van postverstoorde gemeenschappen in boreale bossen meer overeenkomsten vertoonde met de structuur vóór de verstoring, dan het geval was in gematigde bossen. Dit zou kunnen betekenen dat in laagproductieve omgevingen de respons van een gemeenschap op een verstoring minder variabel en daarom beter te voorspellen is dan in hoogproductieve omgevingen.

In hoofdstuk vier heb ik de dichtheid-lichaamsgewicht-relatie (DBM: density–body mass) gebruikt om de veranderingen in de gemeenschapsstructuur na een verstoring te detecteren. Mijn hypothese was dat de helling van de bijbehorende regressielijn vlakker zou zijn indien vooral de kleinere organismen leden onder de verstoring, en steiler indien vooral de grotere organismen geraakt werden. Door op drie tijdstippen (vlak vóór, vlak na en twee maanden na de verstoring) samples te nemen van bodemfauna, ontdekte ik dat de aard van de DBM-relatie de wijzigingen weerspiegelden die de gemeenschapsstructuur onderging in reactie op omgevingsveranderingen. Vlak na een verstoring vlakte de DBM-relatie van de gemeenschap af, met als achterliggende reden dat vooral kleine organismen leden onder de verstoring. Evenzo kon ik aantonen dat gedurende het eerste stadium van herstel de DBM-relatie zelfs nog verder afvlakte, als gevolg van het relatief grote lichaamsgewicht van de pionierssoorten. Dit duidt op de noodzaak om de sample te laten bestaan uit organismen uit uiteenlopende gewichtsklassen. Het is bovendien de eerste keer dat is aangetoond dat de DBM-relatie kan worden gebruikt als een proxy voor veranderingen in een gemeenschapsstructuur. Ik concludeer het hoofdstuk door op te merken dat deze methode kan worden ingezet voor milieukundige biomonitoring.

Aangemoedigd door voornoemde resultaten besloot ik uit te zoeken of the DBM-relatie ook kon worden aangewend om verschillen te detecteren in de structuur van gemeenschappen die voorkomen in gebieden met verschillende productiviteit, met en zonder verstoring. Dit onderzoek wordt beschreven in hoofdstuk vijf. Mijn hypothese was dat gemeenschappen in laagproductieve gebieden een vlakkere DBM-helling zouden hebben dan gemeenschappen in hoogproductieve gebieden, en dat hetzelfde (een vlakke DBM-helling) gold voor verstoorde gemeenschappen. Om dit te kunnen testen, verzamelde ik samples van bodemfauna van een zoutmoeras. Ik nam samples van plots op vier verschillende hoogteniveaus, waarbij elk hoogteniveau een eigen inundatiefrequentie had, variërend van dagelijks tot jaarlijks. De helft van de plots werd begrazen door vee (verstoring). Metingen van de hoeveelheid strooisel bevestigden mijn aanname dat de meeste productieve plots de plots waren die het minst onder water kwam te staan. Uitsluitend tussen de dagelijks en jaarlijks geïnundeerde plots verschilde de helling van de DBM-relatie significant van elkaar, bevestigend dat gemeenschappen in hoogproductieve gebieden een steilere DBM-helling hebben. Het lijkt erop dat een hoge productiviteit niet alle trofische niveaus evenzeer beïnvloedt, wat naar alle waarschijnlijkheid te maken heeft met de inefficiënte energieoverdracht tussen de verschillende niveaus.

In de synthese benadruk ik dat ecologisch herstel eerst helder gedefinieerd dient te worden om vast te kunnen stellen wanneer een gemeenschap zich nu eigenlijk in het stadium van herstel bevindt. Ik adviseer daarbij om voor dat doeleinde pré- en postverstoring condities van controlegemeenschappen als referentie te gebruiken. Daarnaast geldt dat in plaats van te focussen op één soort of één ecosysteemdienst, er verscheidene omgevingsfactoren in beschouwing dient te worden genomen, omdat, zoals door mij aangetoond, zowel soortenrijkdom en –abundantie als de productiviteit en heterogeniteit van een omgeving, de weerstand en het herstel van ecosystemen kunnen beïnvloeden. Ik raad aan om soortensamenstelling eerst te bestuderen in limiterende omgevingen, omdat de stochastische factoren daar een kleinere rol spelen en het dus beter mogelijk is om begrip te krijgen van de mechanistische processen welke soortensamenstelling bepalen. Aangezien kennis daarvan nu nog ontbreekt, doen natuurbeheerders die op voorhand de uitkomst van ecologisch herstel willen schatten, er vooralsnog het beste aan om een fenomenologische benadering te hanteren.

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[1] Good one, Ralf!

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BIOGRAPHY

After my Bachelor of Biology received at the University of Caen, France, I decided to get fully specialised in Ecology and, therefore, attended the University of Rennes, France, and, subsequently, the University of Aix - Marseille, France, where I graduated and obtained a Master in Continental Ecology and Biodiversity. Eager to pursue in the field of scientific research and with a strong interest in community ecology, disturbances and biodiversity, I started a PhD at the University of Wageningen that gave me the opportunity to work on these topics in many different environmental and cultural conditions, from the tropics to the boreal forest. I am now aiming for positions where I could dedicate all my skills to the fields of conservation biology and sustainable development.

Lake Pukaki and Mount Cook (Aoraki)
New Zealand (2011)

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PE&RC PhD Training Certificate

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With the educational activities listed below the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities).

Review of literature (4.5 ECTS)
- Recovery of assemblages following a catastrophic disturbance over a latitudinal gradient (2008)

Writing of project proposal (4.5 ECTS)
- Recovery of assemblages following a catastrophic disturbance over a latitudinal gradient (2008)

Post-graduate courses (4.8 ECTS)
- Nematode course; WUR (2008)
- Consumer resource interactions; WUR (2010)

Laboratory training and working visits (4.6 ECTS)
- Experiments to test methods; WUR (2008)
- Visit to Matty Berg; Vrije Universiteit, Amsterdam (2008)
- Visit to Hannu Fritze; METLA, Helsinki (2009)
- Visit to Noel Tawatao; Universiti Malaysia Sabah (2009)

Invited review of (unpublished) journal manuscript (1 ECTS)
- Diversity and Distributions: community ecology in a savannah (2012)

Deficiency, refresh, brush-up courses (2.8 ECTS)
- Ecological methods (2008)

Competence strengthening / skills courses (2.1 ECTS)
- Competence assessment; WUR (2008)
- Scientific writing; WUR (2011)

PE&RC annual meetings, seminars and the PE&RC weekend (0.9 ECTS)
- PE&RC Day (2007)
- PE&RC Day (2008)
- PE&RC Day (2010)

Discussion groups / local seminars / other scientific meetings (4.8 ECTS)
- Ecological Theory & Application (2007-2012)
- NERN Meeting (2008)
- NERN Meeting (2009)

International symposia, workshops and conferences (4.1 ECTS)
- Forest Ecology Meeting; METLA, Helsinki (2009)
- International Congress for Conservation Biology; Auckland (2011)

Lecturing / supervision of practical's / tutorials; (3 ECTS)
- Wildlife resource management; 15 days (2010)

Supervision of 3 MSc students
- Similarity between communities
- Similarity between communities
- Abundance - body mass relationship

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