Niche and neutral processes in a dry grassland: the example of oribatid mites

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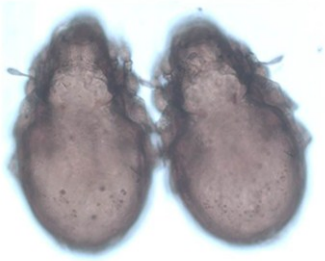

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The most exciting phrase to hear in science, the one that heralds new discoveries, is not 'Eureka! (I found it!)' but 'That's funny...'

Isaac Asimov

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Foreword

This dissertation is a cumulative work of the following published manuscripts. The bibliographic references cited through all chapters are listed together after Chapter 8.

I **Maaß, S.**, Maraun, M., Scheu, S. Rillig, M.C., Caruso, T. 2015. Environmental filtering vs. resource-based niche partitioning in diverse soil animal assemblages. Soil Biology and Biochemistry 85: 145-152. http://dx.doi.org/10.1016/j.soilbio.2015.03.005.

II **Maaß, S.**, Caruso, T., Rillig, M.C. 2015. Functional role of microarthropods in soil aggregation. Pedobiologia 58: 59-63. http://dx.doi.org/10.1016/j.pedobi.2015.03.001.

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1 General Introduction

The huge biodiversity on Earth has fascinated generations of scientists (Morin 2011)and has received more and more attention, unfortunately mostly in terms of increasing biodiversity loss due to habitat loss or environmental pollution. But also the basic mechanisms of how biodiversity is maintained in the respective habitats have been studied intensely. In this work, we aim at studying a group of organisms, namely oribatid mites, to unravel potential mechanisms behind coexistence which results in an amazingly high diversity in a seemingly homogeneous environment like soil. We therefore try to use different theoretical approaches from niche and neutral frameworks which have had a strong impact on ecological research during the last century.

Theoretical background

Before the 18th century, the work of biologists has been rather unordered and natural phenomena were explained rather mystically than scientifically. More descriptive approaches had not started before the 18thcentury and the Church had still a lot of influence on the people's perception of the world. The work of e.g. Carl Linnaeus (1707-1778) who developed the scientific nomenclature, was the starting point for ordered scientific research. He already used definitions and descriptions to highlight the differences among species which can be interpreted as an early attempt of developing concepts of biodiversity and the ecological niche as we know it today (Chase & Leibold 2003).

Additionally, in the 1750s, Georges-Louis Leclerc Count de Buffon (1707- 1788) described that despite of having similar environments, regions differ in their species compositions (later known as Buffon's Law), which is nowadays considered to be the first principle of biogeography. In the 19th century, two names are especially connected to the scientific advances in ecology in Europe: Alexander von Humboldt (1769-1859) and Charles Darwin (1809-1882), the former also laying the foundation for biogeography with his works especially on botanical geography, and the latter with his revolutionizing work on natural selection which is still valid today. But also Alfred Russel Wallace (1823-1913), at the same time, discovered the mechanism of natural selection ('Ternate manuscript' from 1858). Darwin's works on evolution and natural selection can be interpreted as description of the species' niche, however, he used the wording 'line of life' to describe the unique role of a species (Chase & Leibold 2003). In 1877, Karl Möbius (1876-1953) was the first to describe the interaction of different organisms and coined the term 'biocenose' which is also still in use today. Adding to this, in 1896, the Danish botanist Johannes Eugenius Bülow Warming (1841-1924) was the first to officially ask the basic, seemingly trivial but still unanswered questions of ecology: 'Why does each species has its own habitat? How do species congregate to form characteristic communities?' (Warming 1895).

20th century

In 1913, the British Ecological Society was founded with Arthur Tansley (1871-1955), who was influenced by Warming, being its first president (www. britishecologicalsociety.org). The Society aimed at 'promoting and foster the study of Ecology in its widest sense'. Shortly after, in 1915, Victor Ernest Shelford (1877-1968) was involved to found the Ecological Society of America and became its president in 1916 (www.esa.org). These two events marked the beginning of 'ecology' as a distinct field in science.

Another influential theory is Frederic Edward Clements's (1874-1945) climax theory of vegetation (1936) which suggests that after a disturbance the vegetation comes back to a 'climax state' which consists of the vegetation composition best adapted to the local conditions. In contrast to that, in 1917, Henry Allan Gleason (1882-1975) published an 'individualistic concept of ecology' where 'the phenomena of vegetation depend completely upon the phenomena of the individual species' and argued that the distribution of plants follows more randomness rather than being deterministically structured. This approach did not gain popularity until the 1950s, but since then 'species-individualistic' models have become very important in ecology (McIntosh 1995).

However, the idea of the niche was already established by Joseph Grinnell (1877–1939), whose name is also strongly connected to the development of niche based theories. Although the word 'niche' has already been used before by Roswell Hill Johnson (1877–1967, Johnson 1910), it is widely accepted that Grinnell was the first to use this term to discuss the niche of species as we use it today including abiotic, resource and other habitat requirements (e.g. Grinnell 1914, 1917, 1924, Grinnell & Swarth 1913, Soberon & Nakamura 2009, Tingley *et al.* 2009, Wake *et al.* 2009). His most popular publication about the niche-relationships of the Californian thrasher in 1917 was about the niche as an environmental place a species occupies and how this is related to e.g. physiological and morphological plasticity (Chase & Leibold 2003). Although it is officially credited to Georgii Gause (1910-1986) not before the publication of his famous experiments in 1936, Grinnell already alluded the, as he called it 'axiomatic', concept (Grinnell 1917) that two species have to differ in some traits in order to be able to coexist, a concept which is nowadays known as the 'competitive exclusion principle' (Hardin 1960) and one of the fundamental concepts in ecology (e.g. Chesson 1991, 2000). Furthermore, Grinnell also was the person stating the question if communities are saturated with species or if there are 'empty niches' – a question which is still not answered today. Charles Elton (1900-1991), also directly connected to niche theories, was one of the first who studied the interplay between plants and animals, how the behavior is shaped by the environment and he is also assumed to have defined the concept of food chains. Together with his American colleague Aldo Leopold (1887-1948), he introduced the ecological niche in his famous book 'Animal Ecology' (1927). In contrast to Grinnell who focused on the effect of the environment on the species, Elton's idea of the niche was pointed at the functional role of a species within food chains (or food cycles, as Elton called it) and its impact on the

environment. Today, it is assumed that Elton developed his idea more or less independently from Grinnell (Hutchinson 1978, Schoener 1989, Griesemer 1992). However, at that time, the idea of the niche was fully established in ecology. During the following decades, more and more concepts were developed, especially dealing with niches and community structure of plants and therefore using their own terminology. Most of them have been ignored or used as a template for ideas that have been more or less successfully published decades later (for examples see Chase & Leibold 2003). In the 1950s, George Evelyn Hutchinson (1903-1991) succeeded in publishing a more quantitative, and therefore testable, definition of the niche. In a footnote in a paper about limnological studies in Connecticut (1944), he described the niche 'more in Gause's sense than in Elton's' as 'the sum of all environmental factors acting on the organism; the niche thus defined is a region of an n-dimensional hyper-space'. More than ten years later, the n-dimensional hyper-space was termed 'n-dimensional hypervolume' as we still use it today (Hutchinson 1957, Colwell & Rangel 2009): For a given organism, any number (n) of limiting factors which it needs in order to be able to coexist, like e.g. temperature, needs to be defined quantitatively and can be plotted in a space of n dimensions. The space or also range in which a species can exist is defined as the space occupied within this n-dimensional hypervolume (Hutchinson 1957, 1978). Interestingly, a less well developed definition of the niche in multiple dimensions was published by Amyan MacFadyen (*1920) in 1957 (MacFadyen 1957, Chase & Leibold 2003). In his Concluding remarks (1957), Hutchinson also presented two other fundamental definitions: the 'fundamental' and the 'realized' niche. He brought to a point what was obvious in the field, namely that the potentially inhabitable area of a species was mostly greater than the actual occupied space. He therefore proposed that the 'fundamental niche' is the sum of all aspects of the n-dimensional hypervolume in the absence of other species. The 'realized niche' can thus be only part of the fundamental niche and is defined as the niche a species can occupy while facing the presence of other species. With these definitions he also successfully shed light on the importance of interspecific interactions on community structure which had already been pointed out by David Lack (1910-1973) in 1940 (Lack 1940) and from then on gained more and more popularity.

In 1953, Howard Thomas Odum (1924-2002, a student of Hutchinson) and his brother Eugene Pleasants Odum (1913-2002) were the first to write a textbook about the 'Fundamentals of Ecology' (1953), the only one available for a decade. Here they also came up with ecosystem studies and are assumed (Hall 1995) to be the founders of research fields like ecological modeling (Odum 1960), estuarine ecology (Odum & Hoskins 1958) as well as tropical ecosystem ecology (Odum & Pigeon 1970), always intending to find general theories for what they called 'large entities' (ecosystems), so to say: the whole world. At the same time, Robert Harding Whittaker (1920-1980) became very famous for his works on classification of habitats, ordinations, gradient analyses and succession (e.g. Whittaker 1956) which paved the way for multivariate analyses in ecology. For this he was not only awarded several times by the ESA, he also became its vice president in 1970 (www.esa.org). Even more important was that he introduced the term 'β-diversity' alongside with 'α-' and 'γ-'diversity in

1972 (Whittaker 1972). Alpha-diversity is the species richness in a more or less uniform habitat which is assumed to be shaped by competition and other interspecific interactions (like predation) at the community level. Beta-diversity is the change of species richness between two of these samples (species turnover). Gamma-diversity describes the overall diversity of all habitats of the respective region, being the 'consequence of the alpha diversity of the individual communities and the range of differentiation or beta diversity among them' (Whittaker 1972) which is shaped by evolutionary processes such as speciation, migration and also special historical reasons of that particular region.

In the 1960s, the development of theoretical approaches in community ecology flourished (see Kingsland 1995, Cooper 2003), however, the focus was on deterministic processes which is why most of the works during that time belong to the so-called 'traditional community ecology' (Lawton 1999, Brown 1995).

At the same time, another student of Hutchinson and colleague from Lack, Robert H. MacArthur (1930-1972), who was a mathematician interested in biology, started with studies about niches, e.g. in warblers (1958). Together with Levins (1976), he introduced the term 'limiting similarity' which was already partly described by Lack in the 1940s, as a corollary of the competitive exclusion principle, supported by studies from e.g. Hutchinson (i.e. size ratio of boatman, 1959) which claims that there is a limit of how similar species can be at most in order to coexist at equilibrium. Additionally, he co-authored with Edward Osborne Wilson (*1929) the seminal book about the Theory of Island Biogeography in 1967 which is based on their publication about the Equilibrium Theory of Insular Zoogeography a few years earlier (MacArthur & Wilson 1963). This was the turning point from a static viewpoint of niche and other assembly components based on data collected in the field to a 'dynamic' equilibrium based on synthetic approaches to biogeographical processes (see for review Simberloff 1975, Gilbert 1980). The theory supposes that the number of species on an island (also in the broader sense as fragmented habitats) depend on immigration from a source pool (e.g. continent, next suitable habitat patch) and extinction. Both these processes are affected by the distance of the island to the source pool (distance effect). Over time, extinction and immigration reach an equilibrium of species richness. Once a species has successfully colonized an island, the chance of extinction is dependent from island size. The so-called species-area effect says that larger islands offer more potential suitable habitat space which can be colonized. Hence, the chance of extinction due to chance events is reduced. Additionally, the larger the island, the higher the chance that new colonists target the island due to greater number of resources and available habitats and the island may accumulate more species by chance just because it is larger (known as 'target effect'). Finally, the 'rescue effect' describes that the less isolated an island is, the higher is the chance that new individuals reach the island from the source pool and 'rescue' the resident populations from going extinct. This theory has been very influential and is nowadays still of high importance for e.g. conservation biology. It is also a corner stone for a different approach to community assembly studies: it is a neutral model as the identity of species and their interactions are not important. This idea was not completely new at this

point as Motoo Kimura (1924-1994), a population geneticist, published a neutral theory in 1968 which already provided a unifying frame for even earlier studies, e.g. from Wright (1931) (for details see Leigh 2007). He proposed in this theory that each gene, independent of its genotype, is equally likely to enter the next generation. This means, that all genotypes have equal fitness, and changes in allele frequencies are due to migration, mutation and demographic stochasticity (Leigh 2007). As in Hubbell's (*1942) case more than three decades later, this theory evoked controversial discussions (Ohta & Gillespie 1996, Leigh 2007) as on the one hand it offered a simple approach to explain species abundance distributions (e.g. Caswell 1976, Hubbell 1979, 1997, Bell 2000, 2001) but on the other hand ignores what no ecologist would deny: that species identity is important.

21st century

In the years after Hubbell's Unifying neutral theory of biodiversity and biogeography (2001), there was a lot of research going on to prove or falsify this approach (Dornelas 2006, Bell 2001, Hubbell 2001, see review by Chave 2004) and a lively debate has started how valuable this type of theory is. There have been also many attempts to 'improve' it or include more realistic assumptions. However, more and more ecologists see the future in the strength of both, niche and neutral theories, and argue that a synergistic view would increase the overall understanding of how community structures are influenced by all the various processes known (e.g. Adler *et al.* 2006, Thompson & Townsend 2006, Lindo & Winchester 2009, Caruso *et al.* 2012b). Amongst others, Rosindell *et al*. (2012) support to use neutral models a a valuable tool in form of a null model (see e.g. McGill *et al*. 2006, Wennekes *et al.* 2012) and new ideas in regard to the usefulness of null und neutral models. However, Hubbell's Unified Theory of Biodiversity remains the most famous version.

With the seminal work of Leibold *et al.* (2004), the metacommunity concept was brought forward where metacommunities are defined as a set of local communities consisting of multiple potentially interacting species which are linked by dispersal (Hanski & Gilpin 1991, Gotelli & Kelley 1993). Adding to traditional community ecology where the communities are a product of local interactions like competition for resources among all present organisms, the metacommunity concept includes also larger-scale dynamics which are caused by movements of the individuals among communities. Leibold described four main processes which are potentially of major importance for the assemblage of communities: (1) patch dynamics, (2) species sorting, (3) mass effects, and (4) neutral dynamics.

The Patch Dynamic Perspective makes assumptions about communities consisting of multiple species in multiple identical (homogeneous) patches and can therefore be considered to be based on the Equilibrium Theory of Island Biogeography (MacArthur & Wilson 1967). Patch dynamics are based on two assumptions: first, populations have a certain rate of local extinction so that species will go extinct continuously; second, the spread of populations is restricted due to dispersal limitations which differ between the respective species (Holyoak *et al.* 2005). In case of dispersal rates being limited,

dominant species cannot drive other species to extinction which makes coexistence possible. Tilman (1994) and Hastings (1980) already pointed out that microsites can also hold single individuals so that extinction rates can be interpreted as mortality rates and colonization as birth rate and movement. However, the result remains the same – given an appropriate trade-off between colonization (including fecundity) and competitive capabilities of the species, coexistence is possible (Holyoak *et al.* 2005).

In the framework of species sorting, a landscape consists of heterogeneous patches with differing environmental conditions. In the patches, only species which are best adapted to the respective environment can survive there as the abiotic factors have considerable effects on the vital rates of populations and species interactions (Leibold 1998) which results in a community change along environmental gradients (Whittaker 1972). Dispersal is considered to play a role in regard to colonization and enables species to track changes in local environmental conditions. Several studies (e.g. Dobzhansky 1951, MacArthur 1958, Pianka 1966) pointed out that this view is very similar to classical niche theory where abiotic factors have the major influence on community assemblages (Holyoak *et al.* 2005) and purely spatial effects can be neglected (Cottenie & de Meester 2005). However, as Holyoak *et al.* (2005) point out, the predictions of this framework become more appropriate when the influence of dispersal is increased and also mass effects come into play.

The mass effect perspective (Shmida & Wilson 1985) focuses on the impact of dispersal (i.e. immigration and emigration) on local population dynamics which is assumed to operate at higher speed than local interactions between species. Immigration can have strong influences on the respective density of a population and supplement birth rates. Emigration has the opposite effect as it increases the loss of species compared to closed systems, both effects acting independently of habitat heterogeneity (Holyoak *et al.* 2005).

The fourth framework is the neutral perspective which is based on the assumption that all species are demographically equivalent (i.e. birth rate, death rate but also competitive abilities). Diversity patterns are created by random walks and extinctions whereas environmental conditions do not play an important role. Thus, neutral models predict that isolated local community richness inevitably drops to a single species community due to the accumulation of random extinctions (ecological drift, termed by Hubbell 2001). However, this view is also connected to Island Biogeography, as it considers immigration and speciation as well as extinction and emigration as most important parameters influencing species diversity in local communities (Holyoak *et al.* 2005).

Already in 1994, Palmer noticed that were at least 120 hypotheses about how species diversity is maintained. Five years later, Lawton (1999) called community ecology ‘a mess’ being caused by a lack of full comprehension about underlying processes. This hasn’t changes, but nowadays, modern community theory acknowledges that biodiversity is structured by several processes at different hierarchical scales, ranging from populations of one certain species to populations of different species which interact with each other (e.g. prey and predator) and finally whole ecosystems and their

communities (i.e. indirect interactions) (Levin 1992, Chase & Leibold 2002, Holt & Gaines 1993, Hubbell 2001, Holyoak *et al.* 2005, Chave 2013).

Modern community ecology

In the framework of modern community ecology, there are three processes which are assumed to have a major influence on community assembly: environmental filtering (originating from niche based approaches), dispersal (originating from the metacommunity framework (Holyoak *et al.*2005) and brought to attention by Hubbell's neutral theory (2001)) and biotic interaction (e.g. in terms of competition, see review by Wardle 2006). Abiotic factors act as a filter on species' establishment and can also be seen as a series of filters that select for particular traits (Weiher & Keddy 1995, HilleRisLambers *et al.* 2012). The view about the niche has also slightly changed: It is no longer seen as the space of suitable environmental parameters a specimen lives in, but also the impact of the specimen on the environment is considered (i.e. consumption of resources).The idea that species can modify their own environment is not new: Already Darwin included them into his works (1851,1881, Scott-Phillips *et al*. 2014) which has led to respective theories and studies (e.g. Jones *et al.* 1997, Day *et al.* 2003, niche-construction theory (NCT) by Odling-Smee *et al*. 2003, 2013, see review for invertebrates as ecosystem engineeres by Jouquet *et al.* 2006). The so-called ecosystem-engineering is a functionally important class of non-trophic interactions which can have a strong effect on entire communities (Jones *et al.* 1997, Odling-Smee *et al.* 1996, Post & Palkovacs 2009) and hence needs to be discussed in this framework.

Additionally, dispersal limitation restricts the pool of potential colonizers which are able to reach the respective location (MacArthur & Wilson 1967) and the effects of stochasticity become more pronounced when species overlap in terms of limiting resources. At this point, the respective population sizes decrease which results in an amplification of the effects of demographic stochasticity (Lande 1993). Finally, biotic interactions like predation and competition play an important role in terms of selecting for a subset of species that actually coexist in the community (Menge & Sutherland 1987, Wardle 2006, Caruso *et al.* 2013). The relative importance of the factors mentioned above may depend on the prevailing conditions and the respective target organism group of the study. Finally, the effect of disturbance on communities (compare intermediate disturbance hypothesis; Connell 1978) has become increasingly important and needs to be studied in more detail to understand the effects on species interactions and hence diversity.

Most of the scientific community has acknowledged that only studies with an integrated perspective can bring forward our still very patchy knowledge about this basic but definitely not trivial question of how communities are influenced by various factors (Belyea & Lancaster 1999, Leibold & McPeek 2006, Adler *et al.* 2007) which can vary with the observational scale of a study, implying that different

mechanisms may act at different scales (e.g. Levin 1992, Rosenzweig 1995, Maurer 1999, Chase & Leibold 2002).

The aim of this thesis was to learn more about niche and neutral based processes as well as biotic interactions which shape the structure of an Oribatid mite community in a grassland in Brandenburg, Germany, at a scale of cm to several meters. Therefore, different methods based on various theoretical frameworks (i.e. measurement of environmental parameters, null model analysis, stable isotope analysis, body size measurements, etc.) were applied to create a multidimensional insight into this community. We also summarize literature and published data to get insights also into other habitat types sampled at larger scales.

Study area and study design

The study was conducted in a natural reserve in Mallnow, Lebus (Brandenburg, Germany, 52°27.778' N, 14°29.349' E). It is part of the so-called 'Oderbruch', a formerly glacial, now hilly region along the Oder river with dry grassland habitats, representing the northernmost and second largest arid region in Germany (mean annual precipitation: 500mm, mean annual temperature: 8.7°C, Deutscher Wetterdienst 2010). For the last 500 years, this reserve has been managed by low-intensity sheep grazing (Ristow *et al.*2011). This has led to a community which is adapted to high light intensities and relatively high soil temperatures.In general, the plant diversity can be very high locally (e.g., more than 40 speciesin a 10x10m plot) although grasses such as *Festuca* spp. dominate the assemblage. The soil itself is characterized as a calciferous boulder clay and very sandy (Hensen 1995). Along the hill slopes, one can observe relatively steep gradients from sandy clayish soils on the top parts to almost pure sandy soils in the lower parts. These gradients in soil types and hence soil structure and environmental conditions go along with a change in not only vegetation cover but also in soil animal communities. We used a small-scale, spatially explicit sampling design (see Fig. 1.1) to test for the relative contributions of pure environmental, pure spatial and spatially structured environmental factors. Furthermore, by introducing the vertical distribution of species along the soil profile, we were able to test for distinct patterns of environmental filtering and niche partitioning.

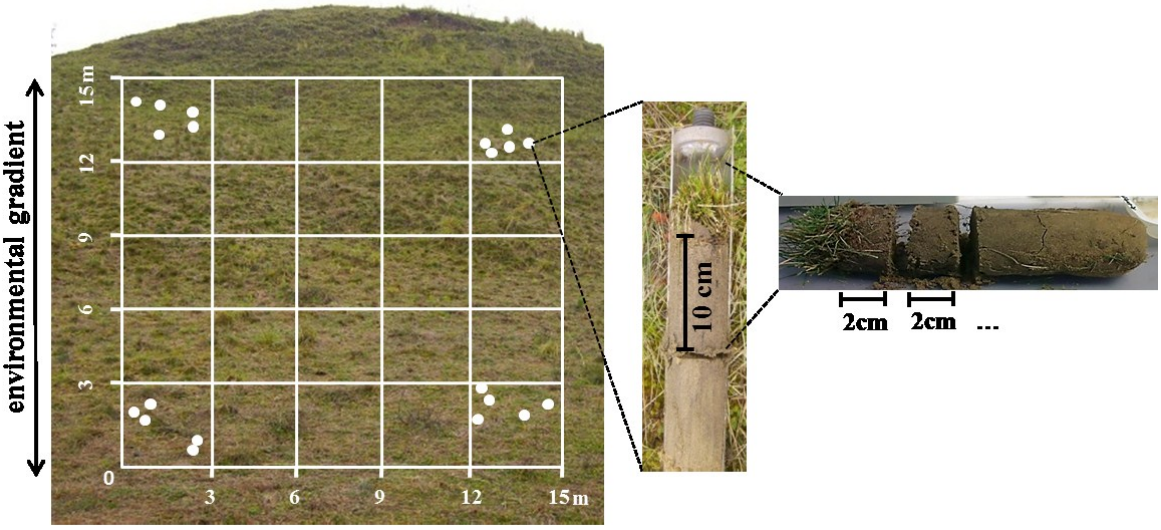

Fig. 1.1 Scheme for sampling design.Up-to downhill direction reflects changes in major environmental variables (water%, content of C and N, pH and soil structure). Soil cores were taken with *Festuca brevipila* on top to define the local community. The first 10cm of the soil core were cut into five 2cm slices for analysis of vertical distribution of oribatid species. Photos: S. Maaß.

In April and October 2012 we randomly took 20 soil core samples (10cm long, 5 cm diameter), each centered on a *Festuca brevipila* individual to define the local community, within each of the two plots of 15x15m along the slope of a hillside. The two plots were about 20m apart and represent spatial replicates in terms of the environmental gradient which is maximized in the up- to downhill direction. Like this, we collected 80 samples in total and additionally recorded the position of each sample in the UTM system. The first 10 cm of each soil core were cut in to five 2cm slices to introduce depth distribution information of the microarthropods into the analyses (for further processing details see chapter 2 and Appendix B).

Soil microarthropod communities

Soils represent highly complex and adaptive systems (Young & Crawford 2004, Crawford *et al.* 2005) which consists of different, highly variable components ranging from physical and chemical properties (Bardgett 2005, Coleman & Whitman 2005) to biological components (Coleman *et al.* 1992). The latter make soil one of the most species rich terrestrial habitats (Anderson 1975, Ghilarov 1977, Stanton 1979) which is why it is usually referred to as 'poor man's tropcial rainforest' (Usher *et al.* 1979). Extensive knowledge about processes, taxonomy and scale is still lacking (Giller 1996) which has been mostly attributed to the 'opaqueness of the system and lack of attractive species" (Usher 1985, Coleman 2011). For a long time, soil organisms have been labeled 'decomposers' which implies a single trophic level acting as recyclers for above-ground material (Sugden *et al.* 2004). In contrast to this, soil communities actually offer the great opportunity of studying various interconnected

processes on various levels of community hierarchy with a broad scale of life-history traits and different size classes (Wardle *et al.* 2003, Rantalainen *et al.* 2005) with some species inhabiting microsites or exhibiting larger ranges of habitat distributions (Wall & Moore 1999). For studying community structures and the factors influencing those, soil offers a vast range of potential target organisms, for example soil microorganisms. They are highly diverse already over short distances, their distribution is structured and their interactions take place at multiple spatial scales (Caruso *et al.* 2012), many of them being dispersal limited (Ettema & Wardle 2002, Mummey & Rillig 2008, Dumbrell *et al.* 2010) but several also show potential for long-distance dispersal (Johnson *et al.* 1996). However, also soil arthropods offer interesting traits and interactions for studying community assembly. Estimates of global biodiversity assume 5-80 million species (Wilson 1992) with most of these species being invertebrates out of which most are arthropods (Giller 1996). In soils, especially microarthropods are highly abundant with Collembola and Acari being the dominating groups.The traits mentioned above for microorganisms are also true for microarthropods (Weigmann *et al.* 1989, Maraun & Scheu 2000, Ettema & Wardle 2002, Schatz 2002, Coulson *et al.* 2003). In this thesis the target organism group is oribatid mites, one of the most abundant microarthropod groups.

Oribatid mites are a very old taxon with first fossils from Devon (380mya) (Shear *et al.* 1984, Norton *et al.* 1988) whereas molecular dating techniques even suggest the Precambrian (appr. 570mya, Schaefer *et al.* 2010). Today, approximately 9,000 species are described worldwide (Subias 2004), the number of species is estimated to be around 100,000 (Schatz 2002, Walter & Proctor 1999). They function as important decomposers in almost all habitats (Weigmann 2006, Maraun & Scheu 2000) and contribute significantly to nutrient cycling in soil systems by feeding on microorganisms, nematodes and organic material and they can facilitate the dispersal of microbial propagules (Behan and Hill 1978, Seastedt 1984, Lussenhop 1992, Maraun *et al.* 1998). They are usually characterized as being k-strategists with a relatively long life cycle (up to three years; Travé *et al.* 1996, Krantz & Walter 2009) and low reproductive output (1-3 generations per year, 1-6 only eggs per clutch, Houck 1994) compared to other soil microarthropods. These two traits suggest that oribatid mites might be sensitive to environmental change and are indeed used as bioindicators (see e.g. review by Behan-Pelletier 1999). However, presumably 10% exhibit a parthenogenetic reproduction (Norton and Palmer 1991, Norton *et al.* 1993), enabling them to act as pioneers and also responding quickly to changing environments. There have been numerous studies about parthenogenesis in oribatid mites (for a summary, see Heethoff *et al.* 2009) and how this can be explained by evolutionary processes. In this context, it has been assumed that co-evolutionary processes between oribatid mites, and decomposer soil invertebrates in general (Salamon *et al*. 2004) and their respective resources are rather weak. This might be caused on the one hand by the fact that dead organic matter cannot exhibit defensive mechanisms against detritivores. On the other hand, Scheu and Setälä (2002) assume that physical isolation of individual microbial species before ingestion is nearly impossible and therefore has prevented the co-evolution between microbivorous microarthropods and the respective prey

species. The broad range of potential food sources for this taxon can be visualized by using stable isotope signatures ($\delta^{15}N$, $\delta^{13}C$). It has been shown that soil and bark-living oribatid mite species can span 5-6 trophic levels (Minagawa & Wada 1984, Post 2002, Schneider *et al.* 2004, Erdmann *et al.* 2007) which has not been observed in other animal taxa. The feeding behavior of most species are to date unknown but would provide important insight into a potential niche differentiation via food resources and would give hints for solving the 'Enigma of soil animal species diversity' (Anderson 1975).

In this context, active dispersal is assumed to happen rather because of seeking for food or potential oviposition sites (Houck 1994) and might be restricted to less than 10 m per year as for many other wingless soil animals (Ghilarov & Perel 1984, Marinissen & Vandenbosch 1992, Ojala & Huhta 2001, Lehmitz *et al.* 2012). Still, it is well known that the vertical migration on a diurnal and seasonal basis might be more substantial (Tarras-Wahlberg 1961, Murphy & Balla 1973). Consequently, dispersal limitation can be assumed to play a major role in the structuring of oribatid mite communities in soil on larger scales (Lindo & Winchester 2009, Caruso *et al.* 2012, Ingimarsdottir *et al.* 2012) and might differ depending on the species' body size (Finlay 2002).

In summary, there are contrasting findings in regard to niche differentiation in terms of food, space and time (Luxton 1972, Kaneko 1988, Siepel & de Ruiter-Dijkman 1993, Walter & Proctor 1999, Schneider *et al.* 2004, Erdmann *et al*. 2007, Caruso *et al.* 2011, 2013) which is why in this thesis we will combine different methods to analyze this in detail.

Thesis outline

Our field study in chapter 2 addresses the topic how environmental filtering affects the soil oribatid mite community in the dry grassland in Brandenburg in comparison to niche partitioning processes. It is demonstrated and discussed why the limiting similarity concept cannot be supported by our data, why the neutral model predictions cannot be rejected and why it is important to analyze species of the same trophic level rather than the whole community when dealing with neutral and niche based approaches.

In chapter 3, we focus on the impact of soil microarthropods on their environment, and especially in the context of soil aggregation. Therefore, we summarize the available literature and discuss potential direct and indirect mechanisms as well as interactions with smaller and larger soil fauna. Additionally, we bring up points about what has hampered closer investigation to date and make suggestions for future studies.

In chapter 4, the focus is on the influence of disturbance on the beta diversity of soil communities and how this can be tested by neutral based approaches. This is done via a synthesis of literature and own data of soil oribatid mite communities.

In chapter 5 we synthesize and discuss all the obtained results.

2 Environmental filtering vs. resource-based niche partitioning in diverse soil animal assemblages

Abstract

Terrestrial invertebrates constitute most of described animal biodiversity and soil is a major reservoir of this diversity. In the classical attempt to understand the processes supporting biodiversity, ecologists are currently seeking to unravel the differential roles of environmental filtering and competition for resources in niche partitioning processes: these processes are in principle distinct although they may act simultaneously, interact at multiple spatial and temporal scales, and are often confounded in studies of soil communities. We used a novel combination of methods based on stable isotopes and trait analysis to resolve these processes in diverse oribatid mite assemblages at spatial scales at which competition for resources could in principle be a major driver. We also used a null model approach based on a general neutral model of beta diversity. A large and significant fraction of community variation was explainable in terms of linear and periodic spatial structures in the distribution of organic C, N and soil structure: species were clearly arranged along an environmental, spatially structured gradient. However, competition related trait differences did not map onto the distances separating species along the environmental gradient and neutral models provided a satisfying approximation of beta diversity patterns. The results represent the first robust evidence that in very diverse soil arthropod assemblages resource-based niche partitioning plays a minor role while environmental filtering remains a fundamental driver of species distribution.

Introduction

The classical view of communities and the assembly processes forming them has historically been dominated by the approaches pioneered by the founders of niche theories. More recently classical theories have been rethought to include stochastic processes suchas those related to stochastic demographic fluctuations anddispersal dynamics, which for example are the only mechanisms postulated in neutral theories (Bell, 2001; Hubbell, 2001). Stochastic processes have also been included in the more general framework of metacommunity theories (Leibold et al., 2004; Cottenie, 2005), which focus on the spatial nature of assembly processes and extend the principles of metapopulation dynamics to community ecology. For example, processes such as dispersal create spatial patterns in species distribution. These spatial patterns do not depend on spatial structure in the distribution ofenvironmental variables although the processes generating these patterns may interact with environmentally driven processes (Smith and Lundholm, 2010). Biotic interaction, too, can create spatial patterns (e.g., segregation of competing species in fairly homogeneous environments), regardless of other spatial processes (Gotelli, 2000; Gotelli et al., 2010). Environmental gradients

determine spatial patterns in species distribution by sorting speciesaccording to their environmental requirements (e.g., dry-tolerantvs. moist tolerant species) and for a long time community ecology has been synonymous with studying species distributions along such gradients (Morin, 2011). These various processes are entangled in nature at multiple spatial scales but a key general point we analyse in this paper is that environmental filtering is one component of niche partitioning dynamics, which might or might not involve resource based niche partitioning due to competition for shared resources (Hubbell, 2005; HilleRisLambers et al., 2012; Adler et al., 2013; Kraft et al., 2014). Interestingly, the point of possible independence of environmental filtering and resource-based niche partitioning has been made both by niche (HilleRisLambers et al., 2012; Kraft et al., 2014) and neutral theorists (Hubbell, 2005) in spite of the fact that several ecologists in practice continue to see niches in the sense of Grinnell, that is to say in terms of species environmental requirements (Chase and Leibold, 2003). Invertebrates constitute most of animal biodiversity and soil is amajor reservoir of this diversity. Soil animal community ecologists, following other animal and plant ecologists (Hubbell, 2001; Dornelas et al., 2006; Ritchie, 2009), for a long time have addressed taxonomically defined assemblages such as oribatid mites, collembolans or nematodes to unravel the mechanisms that allow species coexistence in very diverse systems (Wardle, 2002). Recently, microarthropods have also been investigated within the niche-neutral debates or the more general framework of metacommunity theories (Lindo and Winchester, 2009; Nielsen et al.,2010; Caruso et al., 2012; Salmon and Ponge, 2012). However, inrecent years studies based on stable isotopes and molecular genetics have clearly shown that assemblages such as oribatid mites or collembolans actually consist of species that can range in diet from being decomposers of low quality organic matter to being top predators of nematodes (Schneider et al., 2004; Heidemann et al., 2011; Maraun et al., 2011). This fact implies a strong bias of previous studies in terms of how observed patterns can inform on underlying mechanisms. For example, if we test neutral theories against niche partitioning theories, we should test these within trophic levels (Hubbell, 2005), which challenges previous studies (Lindo and Winchester, 2009; Nielsen et al., 2010; Caruso et al., 2012; Gao et al., 2014). In general, there is little theoretical and empirical support for the hypothesis that soil animal communities are structured by niche dynamics based on competition (Wardle, 2006; Gao et al., 2014), although several studies have shown that microarthropod communities are sorted by environmental gradients (Auclerc et al., 2009; Lindo and Winchester, 2009; Salmon and Ponge, 2012). We addressed this general point by focussing on diverse soil oribatid mite assemblages from a dry grassland using a spatially explicit sampling design that allowed us to minimise dispersal processes and focus on environmental filtering and niche partitioning based on food resources. Instead of focussing on taxonomic assemblages, we used the stable isotopes ratios $^{15}N/^{14}N$ and $^{13}C/^{12}C$, and for the first time focus community analysis on trophic assemblages within which competition for shared resources could be a key process. To further characterise species in terms of traits that can be related to competition for resources, we quantified body size and depth distribution and then defined a trait matrix. We used these data to test the

hypothesis that species that were closer in space and time were more dissimilar and vice-versa (limiting similarity concept) than expected by chance. The assumption is that limiting similarity and/or trait trade-offs should be observed if resource based niche partitioning is a mechanism through which species coexist locally while competing for shared resources. Still, resource-based niche partition and environmental filtering may act simultaneously. Thus, species could also be sorted along environmental gradients either in relation to the measured traits or not. In fact, environmental filtering and resource-based niche partition could also be decoupled if competition is not taking place or is of minor importance. The rationale behind the test of these hypotheses is that demonstrating a clear link between trait differences and environmental distance is a key premise to unravel the mechanisms that allow species coexistence in rich communities (Adler et al., 2013).

Materials and methods

Study area and sampling strategy

This study was conducted in dry grassland in a natural reserve in Mallnow, Lebus (Brandenburg, Germany, 52°27.7780' N, 14°29.3490'E). This reserve has been managed by low-intensity sheep grazing for at least 500 years and is dominated by *Festuca brevipila* (Poaceae).There are areas where grazing may not occur for one year or longer and plant diversity can be very high locally (e.g., > 40 species in a 10 x 10m plot) although grasses such as *Festuca spp*. dominate the assemblage. In these areas, in April and October 2012 we took soil core samples (local communities) within two undisturbed plots of 15 x 15 m along the slope of a hillside, with the two plots about 20 m apart. The two plots represented spatial replicates of a steep soil textural gradient running from the sandy-loamy soil uphill to highly sandy soil downhill. Main soil parameters such as pH, water content, organic C and N varied along the gradient, in some case with remarkable variation (Supplementary Material, Table B S1). Sampling was replicated in the two main seasons (spring and autumn). To standardise the local soil arthropod community, we took soil cores (5 cm diameter, 10 cm deep) centred on the grass *F. brevipila*, which was by far the most abundant species in the area (in some case cover > 70%). Twenty randomly positioned samplesper plot were collected in each season (total of 80 local communities) and the position of each sample was recorded in the UTM system.

Sample processing and analysis

Each soil core was cut into five 2 cm slices to quantify species depth distribution. However, the soil core was the main unit of analysis and we defined the local assemblage as the species inhabiting this unit. Eventually, each species was assigned a depth score based on the weighted average of its depth distribution and depth was treated as a species trait. The soil fauna was extracted ina Macfadyen

apparatus for two weeks. All arthropods were preserved in 70% ethanol and the adult oribatids morphologically determined to species level (Weigmann, 2006). Body lengths were measured for each individual under a dissecting microscope (Leica M165,Wetzlar, Germany) using the software LAS. Each species was assigned a size score based on the average length obtained from a number of replicated measurements (mean number of measurements per species = 85; median number of measurements perspecies = 30). Soil water content was measured as the difference between the weights of fresh vs. dried soil (soil dry weight, SWD), with samples collected at field capacity. Soil pH was measured in a soil-water suspension, where 3 g of soil and 15 ml distilled H_2O were mixed and stirred. The measurement was conducted in the supernatant until the value remained constant. Organic carbon (C) and total nitrogen (N) were measured by direct combustion of 30 mg of soil in a Euro EA Element Analyzer (HEKAtech GmbH, Wegberg, Germany). Mean Weight Diameter (MWD) was calculated as the weighted sum of the proportion of soil particles and aggregates in each size class (2-4 mm, 1-2 mm,0.5-1 mm and 0.2-0.5 mm), determined by dry sieving of the soil.

Stable isotope analysis

Specimens were transferred into tin capsules. Rare (e.g. *Carabodes willmanni*) or smaller-sized species (e.g. *Microppia minus*) required the pooling of several individuals to reach the biomass necessary to the analysis. After drying at 60 °C for at least 12 h, samples were reweighed and stored in a desiccator until further analysis. The same procedure was used to prepare samples of nematodes, extracted from fresh soil by using a modified Baermann funnel method. Soil, mosses, lichens, roots, and plant material were ground and subjected to the same procedure (root and plant material 1.0-1.5 mg, soil 34.1 - 35.3 mg).We analysed these organismsand material to obtain baseline values of different potential food sources for oribatid mites (Supplementary Material B). A coupled system of an elemental analyzer (Euro EA 3000, Euro Vector S.p.A.: Milano, Italy) and a mass spectrometer (Delta V Plus ThermoElectron; Bremen, Germany) was used to analyse the $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios (Reineking et al., 1993). The primary standard for ^{15}N was atmospheric nitrogen whereas acetanilide (C8H9NO, Merck, Darmstadt, Germany) served for internal calibration. Vienna PeeDee Belemnite (V-PDB) was used as a primary standard for ^{13}C. See also Fischer et al. (2010), Maraun et al. (2011), Pollierer et al. (2009), and Schneider et al. (2004) for further details.

Data analysis

We used stable isotopes to focus on a diverse but narrowly defined trophic assemblage. We based the definition of ‘relatively narrow trophic assemblage’ on the concentration of ^{15}N, which increases from food sources to consumers (Deniro and Epstein, 1981; Peterson and Fry, 1987; Scheu, 2002). The enrichment of ^{15}N varies with diet, especially in generalists, but despite this variation, an average enrichment of 3.4‰ is commonly used to define trophic groups (Post, 2002). The concentration of ^{13}C isusually associated with the analysis of ^{15}N because ^{13}C reflects the basal food source (Deniro and

Epstein, 1981; Peterson and Fry,1987; Post, 2002). The variance of stable isotope signatures reflects the dietary niche width of consumers (Bearhop et al., 2004), which led some authors to define the concept of isotopic niche (Newsome et al., 2007). Eventually (see results) we could define aset of 18 species that potentially competed for fungal resources, and we focused our analysis on this assemblage. In order to visualise and quantitatively summarise the multivariate covariation of environmental variables (Organic C, N, C:N, Water, pH, Mean Weight Diametre of soil particles) and majorgradients, we performed a Principal Component Analysis (PCA) on the correlation matrix of the variables (Legendre and Legendre, 1998; Gotelli and Ellison, 2004). We used PCA axes as environmental correlates of species distribution to eliminate collinearity in predictors (Gotelli and Ellison, 2004). Given the small scale of the study and all else being equal, we used a modelling strategy consisting of several steps to test the general hypothesis that species closer in space and time were more dissimilar in terms of traits related to competition for resources (limiting similarity concept): if resource based niche partitioning is a mechanism through which species coexist locally while competing for shared resources, then limiting similarity or trait trade-offs should be observed (HilleRisLambers et al., 2012; Adler et al., 2013). In order to test this hypothesis, we first used a multivariate regression approach based on RDA (Borcard et al., 1992, 2004; Legendre and Legendre, 1998) to empirically define the spatialand temporal niches of each species. We Hellinger transformed raw data to meaningfully apply RDA, which is PCA-based (Euclidean space), and ensure no inflation of the weights of rare species (Legendre and Gallagher, 2001). The spatially explicit and seasonal sampling design together with the measurement of several crucial environmental variables allowed us to model species distribution as a function of both spatial and environmental factors, and changes between the two sampled seasons. We used the well established method of principal coordinate analysis of neighbor matrices (PCNM; Borcard and Legendre, 2002) to define a set of spatial factors that parsimoniously accounted for patterns in species distribution. The final set of PCNM vectors was defined using a multivariate extension of the Akaike information criterion (AIC; Dray et al., 2006). Environmental factors were soil water content (% dry weight), pH, organic C, total N, the C:N ratio, and the Mean Weight Diameter of soil aggregates, used as a proxy for soil structure (Caruso et al., 2011). We used the species scores of the statistically significant axes of the RDA model to define species niches: by definition, the Euclidean distance between any two species in the vectorial space defined by RDA axes reflects predicted distances inspace, seasons, and environmental conditions: the further apart any two species are in the RDA space the further apart these species are in space, time, and average environmental characteristics of the patches they colonise. We also used permutational tests to test for the effects of spatial and environmental factors, including partial effects (i.e. testing for one factor while statistically controlling for other factors). Once we defined the RDA model-based spatial, temporal and environmental position of species (Grinnellian niche), we used body size and depth distribution together with the $^{15}N/^{14}N$ and $^{13}C/^{12}C$ signature to define a species trait matrix. After data standardization and calculation of Euclidean distance, a trait distance matrix of species was

obtained. We finally used a Mantel test to test the hypothesis of a negative correlation between the trait distance matrix and the distance matrix based on space, season, and environment: we expected a negative correlation under the limiting similarity hypothesis because the more similar species are in traits involved in competition the more distant species should be in their Grinnellian niche. In practice, species minimize spatial and temporal coexistence to avoid competition and at the same time can coexist locally if they differ in key traits. Conversely, the closer species are in terms of spatial, temporal and environmental position the less similar they should be in terms of traits involved in competition. We used the R packages vegan, spacemakeR and ade4 for all multivariate analyses (Chessel et al., 2004; Dray et al., 2006; Oksanen et al., 2009). We completed our analysis with a neutral model, based on the null assumption that trophically similar species are not involved in resource-based niche partitioning when they come together to form assemblages. To fit a general neutral model, we used the formula for multiple samples and a PARI/GP code (Etienne, 2007) to estimate neutral model parameters theta (diversity) and I (immigration rate). Afterwards, we used the PARI/GP function urn2.gp (Etienne, 2007) to create 4999 neutral communities based on the estimate parameters. We applied this approach to the following data sets: all species across all trophic levels (spring and autumn, respectively), and just fungal feeders (spring and autumn, respectively). The simulated communities were used to build a null distribution of beta diversity values. We quantified beta diversity (BD) following Legendre and De Cáceres (2013): the sum of species variances in the species by site matrix (with usual correction terms for unbiased estimates of variance). Data were Hellinger transformed (Legendre and Gallagher, 2001). The observed value of BD was compared to the null distribution: if observed BD was within the 95% interval of the simulated data sets, the neutral model could not be rejected at $p < 0.05$ (Maaß et al., 2014).

Results

Environmental variation

PCA of environmental variables (Fig. 1) summarised more than three quarters of total variation in the first two axes. Although all variables have some effect on all PCA axes, PC1 (53%) described a main gradient mostly due to organic matter (organic C and total N) and soil structure (Mean Weight Diameter, MWD) while PC2 (24%) mostly accounted for a negative covariation between water content and C:N ratio. Consistently with the construction of our sampling strategy, the gradients were maximised along the up-to down-hill direction, with some variation between the two sampling plots (Supplementary Material, Table B S1): the gradient in organic matter and soil structure was more pronounced in Plot 1 while the negative correlation between water and C:N was more pronounced in Plot 2. There was no significant difference between spring and autumn samples for either plots (Supplementary Material, Fig. B S1). Absolute variation in individual soil variables was remarkable in

some case: for example, organic C content ranged from 0.15 to 3.49%, total N from 0.01 to 0.26%, and pH from 4.8 to 8.9, and these ranges were comparable between the two plots.

Oribatid mite assemblage and isotopes

In total, we collected 2397 adult Oribatids of 33 species belonging to 18 families. The most abundant species in both seasons were *Liebstadia pannonica*, *Punctoribates punctum* and *Peloptulus phaenotus*. There were five species (*Achipteria coleoptrata*, *C. willmanni*, *Trichoribates novus*, *Galumna obvia*, and *Minunthozetes semirufus*) that were present with few individuals (1-4) only in one of the two seasons. Rarefaction curves (not shown) confirmed thatthe sampling effort was sufficient to describe the overall richness ofthe oribatid community. We obtained ^{15}N and ^{13}C data for 28 species (Supplementary Material, Fig. B S2 and Table B S3). *M. minus* and *Porobelba spinosa* showed the highest ^{15}N signatures whereas *C. willmanni* had the lowest ^{15}N signature. Three species (*M. semirufus*, *Tectocepheus velatus sarekensis*, *Scutovertex sculptus*) had very similar ^{15}N signatures comparable with the root signatures while mosses, lichens, and nematodes were about one trophic level below their potential consumers/predators (Supplementary Material, Fig. B S2 and Table B S1). Overall, the stable isotope analysis and relevant literature (Schneider et al., 2004; Pollierer et al., 2009; Fischer et al., 2010; Maraun et al., 2011) allowed us to group the oribatid mite community into five trophic groups (predators, fungal feeders/secondary decomposers, decomposers, lichen feeders and species with endophagous juveniles/tunnelers, see Supplementary Material). However, for *T. novus*, *Passalozetes perforates* and *M. semirufus*, the group affiliation was not clear. We consider *P. perforates* to be a mycophagous species and *M. semirufus* a moss feeder but definitive evidence is missing. The feeding preferences of *T. novus* remain unclear. Based on these data, we defined a group of 18 species (Table 2.1; Supplementary Material, Table B S2) in the broad category fungal feeder/secondary decomposers: several of these species can in principle compete for shared resources. We focused our modeling and hypothesis testing on this assemblage.

Table 2.1 Species list of fungal feeders and the species codes used in Fig. 2.2 (RDA ordination plot). Mean (±SE) number of individuals (m^2) in the two seasons is reported for each species. See Supplementary Information (Table B.S2) for a list of all oribatid mites.

Species	Species code	May '12	Oct '12
Tectocepheus velatus alatus	s1	<10	<10
Punctoribates punctum	s2	2484 ± 463	1873 ± 372
Peloptulus phaenotus	s4	2063 ± 387	1338 ± 194
Liebstadia pannonica	s5	3236 ± 725	5096 ± 1231
Oppiella nova	s8	420 ± 144	688 ± 265
Eupelops tardus	s11	357 ± 192	408 ± 120
Scheloribates laevigatus	s12	510 ± 153	688 ± 196
Galumna obvia	s13	0	51 ± 31
Scheloribates quintus	s14	280 ± 79	726 ± 194
Pergalumna nervosa	s15	153 ± 49	1057 ± 239
Protoribates capucinus	s18	115 ± 43	178 ± 76
Trichoribates incisellus	s22	153 ± 45	191 ± 51
Eupelops occultus	s23	280 ± 159	140 ± 66
Suctobelbella sarekensis	s24	255 ± 181	191 ± 79
Liacarus coracinus	s25	229 ± 105	115 ± 43
Chamobates birulai	s26	26 ± 18	26 ± 26
Dissorhina ornata	s30	1707 ± 630	127 ± 79
Achipteria coleoptrata	s32	<10	<10

Hypothesis testing

The RDA showed that PCNM-based spatial factors and environmental factors (PC1 and PC2 from PCA of environmental variables, see Fig. 2.1) could account for 31% of total community variation, the total effect of these factors being statistically significant at $p < 0.01$ following a permutational test. However, variance partitioning showed that 21% of this variation was attributable to spatial patterns in the environmental variables while 10% were accounted for by statistically significant (partial RDA, $p < 0.05$) spatial patterns not related to environmental variation. Less than 1% of variation was explainable in terms of environmental variation that was not spatially structured and this variation was not statistically significant. A RDA based just on environmental factors (i.e. implicitly including spatial structures) accounted for 22% of total variation, the effect of the environment being significant at $p < 0.01$. To test for the factor season, we extracted the residuals of the first, main RDA model and submitted these to a PERMANOVA test, which showed a significant effect of season ($F_{1, 78} = 4.17$, $p < 0.01$). Introducing the season factor in the RDA increased total explained variation to 44%. A permutation test showed that the first five RDA axes were significant at $p < 0.01$ and these axes were therefore retained to define the niche space (i.e., based on spatial and temporal distance, which we, given our result, basically understand as the environmental or Grinnellian component of a species

niche). A plot of the first two RDA axes (Fig. 2.2) and the main environmental gradients (based on PCA of environmental organic matter and soil structure. This gradient is associated with a certain species set while the second axis is driven by a second gradient due to the negative covariation of soil water and C:N. This second gradient is associated to a species set other than that associated to the first gradient. Size and the ^{15}N signature were negatively and significantly correlated with each other but scarcely correlated with the major environmental gradients, although a positive and significant correlation was detected between ^{15}N and RDA1 (Fig. 2.3). After standardization, a Euclidean distance matrix was calculated from the Grinnellian niche space and correlated to the species trait distance matrix (based on ^{15}N, ^{13}C, size and depth distribution) via a Mantel test: no significant correlation was found (Fig. 2.4), which is inconsistent with the limiting similarity hypothesis. None of the tested assemblages differed significantly from a neutral model for beta diversity (Supplementary Information,Fig. B S3; whole assemblage, spring: $p = 0.10$; whole assemblage autumn: $p = 0.16$; fungal feeders spring: $p = 0.07$; fungal feeders autumn: $p = 0.10$, see Table B S4 for the estimate of neutral model parameters). However, in all cases we observed assemblages with beta diversity higher than expected under neutrality (Fig. B S3), and this trend was more pronounced in the fungal feeder group.

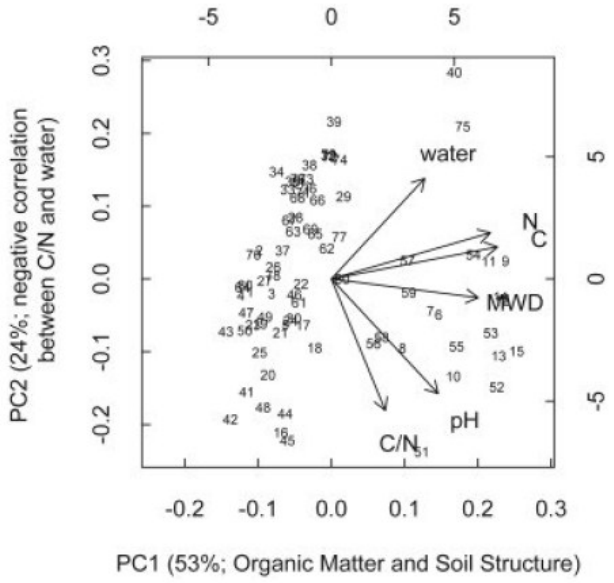

Fig. 2.1 Principal Component Analysis (PCA) of the correlation matrix (z-scores) of environmental variables: 77% of total variance can be summarized in the first two axes. PC1 (53%) described a main gradient in organic matter (organic C and total N) and soil structure (Mean Weight Diameter, MWD); PC2 (24%) described a negative covariation between water content and the C:N ratio. The vectors associated with the variables are based on PCA eigenvectors (i.e. variables loadings on PCA axes). Numbers represent soil samples.

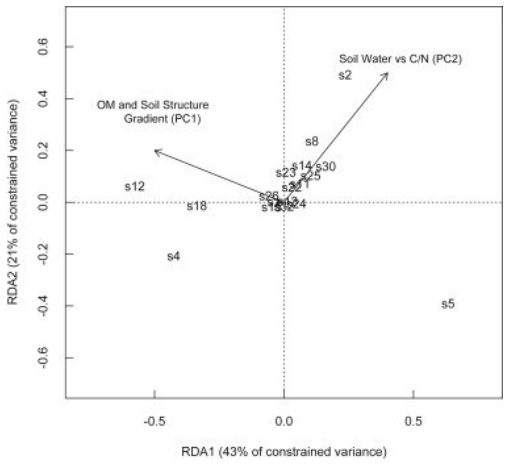

Fig. 2.2 First two RDA axes based on a model including spatial vectors, environmental gradient and seasons. Only species points are displayed to show which species are associated with the two environmental gradients. See Table 1 for species labels. This RDA model accounted for 44% of total species matrix. The RDA axis 1 is driven by a gradient of organic matter and soil structure (PC1 of Fig. 2.1). RDA axis 2 by a contrast between water content and C:N ratio (PC2 of Fig. 2.1).

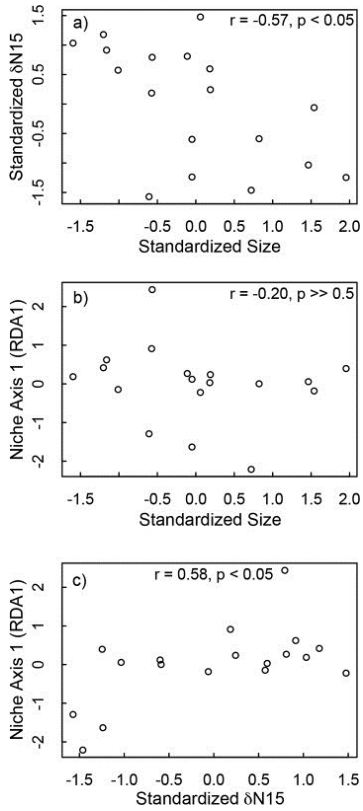

Fig. 2.3 a) correlation between size (x-axis) and species trophic position (15N, y-axis) is negative and statistically significant; b and c), correlation between species scores of RDA 1 (y-axis; see Fig. 2.2) and size (panel b) or 15N (panel c), on the x-axis. RDA1 is a proxy for the environmental, spatial and temporal (seasonality in this case) components of niche. No or weak correlation is observed in panel b and c respectively. Similar figures were drawn (but now shown here) for the first five RDA axes, with the same result. Each data point represents a species.

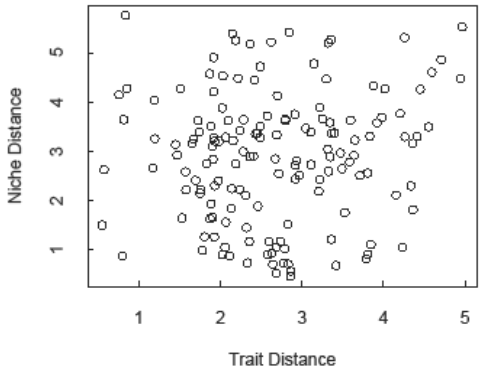

Fig. 2.4 Niche distance between species is based on the species scores of the statistically significant axes of an RDA (spatial vectors, seasons, and environmental variables). The Euclidean distance between any two species in the vectorial space defined by RDA axes reflects predicted spatial, temporal and environmental distances: the further apart any two species are in this space the further apart these species are in terms of their niche.This RDA-based Euclidean distance matrix was correlated to the species trait distance matrix (based on 15N, 13C, size and depth distribution) via a Mantel test: the Fig. and test show a remarkable lack of correlation, which is inconsistent with the limiting similarity hypothesis.

Discussion

Differences between environmental filtering and competition

In recent works investigating the role of deterministic and stochasticdrivers of soil organism community structure (Lindo and Winchester, 2009; Dumbrell et al., 2010; Nielsen et al., 2010; Caruso et al., 2012; Gao et al., 2014; Beck et al., 2015) researchers contrasted environmental filtering, typically equated to niche dynamics, with spatial factors not dependent on patterns of environmental variation, sometimes called 'pure' spatial factors. These spatial factors are often understood as the effect of dispersal and/or demographic fluctuations in neutral assembly processes; but several ecologists, including those cited above, also recognise that these factors do not necessarily represent stochastic spatial factors (Smith and Lundholm, 2010; Anderson et al., 2011; Caruso et al., 2012). Besides the problem of the interpretation of spatial factors, a key but not often addressed aspect of this central topic is that environmental filtering may imply competition for resources but does not necessarily imply resource-based niche partitioning dynamics: this is a point on which niche and neutral theorists may agree (Hubbell, 2005; HilleRisLambers et al., 2012), although from very different perspectives. At certain scales environmental filtering is compatible with neutral processes because in neutral dynamics competition for resources between species is not a driver of community structure while individuals, regardless of the species they belong to, must still exploit resources and fit their environment (Hubbell, 2005). Different species can therefore come together into a local community if they are adapted to the environmental conditions of the locale, and in this sense the

environment will tend to select for similar species (e.g., shade-tolerant species in shaded environments). A neutrally assembled local community can therefore be environmentally filtered at certain scales while being neutral at scales at which competition among species has classically been postulated to structure communities (Hubbell, 2005; Etienne, 2007). It is in this general framework that we interpret our results: when biotic interactions start to be a fundamental driver and predictor of community structure neutral theories should be abandoned. Specifically, neutral theories directly contrast with resource-based niche partitioning processes. A first consideration is therefore that not all biological interactions should be considered, especially multitrophic interactions, which, apart from possible future developments, are usually outside the realm of application of neutral theories (Hubbell, 2001, 2005). For the first time, we have focused on a soil animal assemblage that was trophically defined by the use of stable isotopes of N and C. In doing so, we could start from the empirically validated assumption that competition for resources is a fairly valid possibility within the analysed assemblage. The small scale of the study also allowed us to assume that dispersal limitation, while still a possible factor given the size of our animals (Ettema and Wardle, 2002), should play a minor role. As shown by the analysis of the soil, communities were sampled along steep environmental gradients in a very short distance. Accordingly, we observed a strong, spatially structured correlation between environmental gradients and the structure of the species assemblage. We can therefore conclude that the assemblage was subjected to environmental filtering. This result might imply that species living in different environmental patches spatially segregate to avoid competition locally. However, by no means can this result in itself be considered evidence of resource based niche partitioning, which should also explain coexistence locally. This is an observational study: in order to reject non-neutral dynamics and find strong evidence of resource-based niche partitioning,we should have rejected neutral prediction of beta diversity and detected patterns consistent with the limiting similarity hypothesis along the environmental gradient, including the localscale of the assemblage inhabiting individual soil cores. Instead, neither could we reject neutral predictions of beta diversity nor could we find patterns consistent with the limiting similarity hypothesis. Observed beta diversity of the assemblage was higher than neutral predictions, as usually expected under environmental filtering (Dornelas et al., 2006; Caruso et al., 2012), but not significantly higher, with fairly high p-values in all cases but one. Species more similar in terms of spatial and seasonal distribution were not more dissimilar in terms of isotopic signature, size, and depth distribution. In theory, size could here be related to competition if we make the classical assumption that species at similar trophic positions avoid competition by differing in size: in this way competing species have access to similar resources in different places (i.e., colonization of differently sized soil pores; Weis-Fogh,1948; Ritchie, 2009; Turnbull et al., 2014). The local community of our study is the cylindrical soil core used as sampling unit. In this relatively small locale, species that feed on similar resources and have similar size could still partition space by dwelling at different average depths but species weighed mean average depth was not atrait that could explain coexistence.

Niche partitioning mechanisms and competition

In spite of all the efforts we made to identify the possible dimensions along which competing species could partition their niches, none of these dimensions or their combination provided us with evidence of limiting similarities indicative of resource-based niche partitioning. In fact, the only pattern we have found is a slightly positive correlation between trophic position ($d^{15}N$ value) and the major environmental gradient along which the community is structured. However, the correlation seems made up by three low $d^{15}N$ values and one high $d^{15}N$ value, with the other points scattered in a fairly random manner. In any case, even if we accepted the validity of this correlation, this result would not support the limiting similarity hypothesis. We observed a significant fraction of spatial variation that was not related to environmental gradients. This variation can be due to stochastic but spatial factors such as dispersal, or it could be due to biotic interactions such as predation or competition. Predation can mediate competition by controlling the population of the more competitive species (Chase and Leibold, 2003): predators may spatially structure their prey but in the case of oribatid mites, and differently from collembolans, there is strong evidence that predation is not a strong factor controlling populations (Peschel et al., 2006). Competition and resource based niche partitioning could still play some role because we measured the traits that were most logically expected to be key traits for coexistence, but in fact we could have missed some important aspects. For example, there are limitations in the stable isotope markers we employed: the ^{13}C signature of animal fatty acids has now been demonstrated to be a finer marker for a detailed differentiation of fungal feeders (Ruess and Chamberlain, 2010; Pollierert al., 2012) while with the method we employed we have been able to isolate a narrowly defined trophic assemblage (i.e. guild) but we might not have been able to differentiate trophic differences within this assemblage. Natural variability in isotopic signatures may also suggest high intraspecific variability in feeding strategies. This could be especially true for different developmental stages. We are aware of data at this level for one species only (Schneider et al., 2004) and these data suggest small differences between adults and nymphs but other species could definitely vary their diet depending on developmental stage. The interesting point is that high intraspecific variability can imply broad interspecific niche overlaps at the species level, opening the way to neutral assembly processes. The same arguments apply to temporal variation in species soil depth and may imply a theoretical scenario for which levels of competition vary in space (both horizontally and vertically) and time as a function of fluctuations in population densities. Another limit of our study is that we might not have included all the species relevant to the analysed assemblage. We focused on fungal feeder/secondary decomposer oribatid mites, which is by far the most diverse and abundant group of microarthropods together with collembolans. However, there are other fungal feeders/secondary decomposers in soil, for example collembolan species. We cannot exclude that competition for resources would have been a strong driver of an assemblage that included all the species competing for a limited set of resources. Finally, our multivariate analysis suggested that seasonal variationis potentially a key niche dimension although our study is deficient in terms of

temporal replication. Species competing for similar resources could peak at different times of the year to avoid competition, basically for the same principle for which competing species may segregate spatially. Nevertheless, only future studies will tell whether the observed temporal patterns depend on a temporal form of environmental filtering (e.g. seasonality) or resource based niche partitioning mediated by temporal fluctuations in resources and population densities, or both. Overall, our results indicate that environmental filtering and resource-based niche partitioning can be decoupled in soil animal assemblages while the burden of the proof of resource-based niche partitioning in soil community still remains with the ecologist.

Acknowledgements

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3 Functional role of microarthropods in soil aggregation

Abstract

Soil aggregation has received a lot of attention in the last years; however, the focus was mostly on soil microorganisms or larger soil fauna, especially earthworms. The impact of the large group of microarthropods, e.g. Collembola and Acari, is nearly unknown and hence underrepresented in the literature. Here we propose and discuss potential direct and indirect mechanisms of how microarthropods could influence this process with the focus on collembolans, which are in general a relatively well studied taxon. Indirect mechanisms are likely to have larger impacts on soil aggregation than direct effects. The variety of indirect mechanisms based on the provision of organic material like fecal pellets, molts and necromass as food source for microorganisms is high and given available evidence we propose that these mechanisms are the most influential. We highlight the need for overcoming the challenges of culturing and handling of these animals in order to be able to design small scale experiments and field studies which would enable us to understand the role of the different functional groups, their interaction with other soil fauna and the impact of land use practices on soil aggregation.

Introduction

Soil structure plays a critical ecosystemic role in biogeochemical processes (e.g. Jastrow, 1996), water infiltration, gas exchange efficacy, and resistance against erosional loss, and influences the performance of soil biota, including roots (Oades, 1984, Miller and Jastrow, 1992, Hartge and Stewart, 1995 and Rillig and Mummey, 2006). Soil structure is often referred to as the arrangement of different macro- and microaggregate size fractions (organic/mineral complexes of >250 µm or <250 µm, respectively) and the corresponding pore spaces (Hartge and Stewart, 1995 and Rillig and Mummey, 2006). In hierarchically structured soils, organic matter serves as the main binding agent to form and stabilize aggregates (Tisdall and Oades, 1982), but additionally, soil texture, soil microorganisms, roots, inorganic binding agents, the predominant environmental conditions, and the soil fauna are important for this process (Dexter and Horn, 1988 and Rillig et al., 2015).

While soil fauna is generally acknowledged as being important for soil aggregation, direct empirical evidence is scarce for microarthropods, including mites and collembolans, the two most abundant and diverse groups. This is surprising given that these animals can occur at high densities, and given their role in the processing of organic matter via chemical, physical and biological mechanisms (Lee and Foster, 1991 and Wolters, 2000). We are only aware of two studies that have experimentally quantified the impact of Collembola on soil structure (Siddiky et al., 2012a and Siddiky et al., 2012b);

these experimental data, however, revealed an effect size comparable to that of much more thoroughly studied soil biota, such as fungi. These experiments should be extended to the field as this might also be of agricultural interest.

Among the various groups of soil biota, especially the effects of mycorrhizal fungi, bacteria, earthworms, and termites have been studied intensely (e.g.; Lee and Foster, 1991, Oades and Water, 1991, Bossuyt et al., 2005, Pulleman et al., 2005, Rillig and Mummey, 2006 and Velasquez et al., 2007). It is known that the excretion of e.g. polysaccharides by bacteria and the physical enmeshment of soil particles by fungal mycelia have a positive effect (see e.g. Lynch and Bragg, 1985, Oades, 1993, Tisdall, 1994b, Degens, 1997 and Rillig and Mummey, 2006). Larger soil animals like earthworms and termites directly affect soil structure by their burrowing activities and by the digestion and excretion of relatively large amounts of organic material and soil particles, which might also lead to increased soil aggregation (e.g. Lee, 1985, Lee and Foster, 1991 and Lavelle, 1998; or see review by Tisdall, 1994a, Tisdall, 1994b and Six et al., 2004).

Given this striking asymmetry in our understanding of biotic contributions to soil aggregation, we here propose and discuss potential mechanisms for Collembola, which are also likely applicable to other soil microarthropods. We distinguish between direct and indirect effects (Fig. 1); however all the mechanisms we discuss would in reality take place simultaneously and in interaction with each other. As the collembolan *Folsomia candida* is very well studied, especially with regard to properties that might be involved in mechanisms of soil aggregation, we base our discussion mostly on this species, but we believe without much loss of generality.

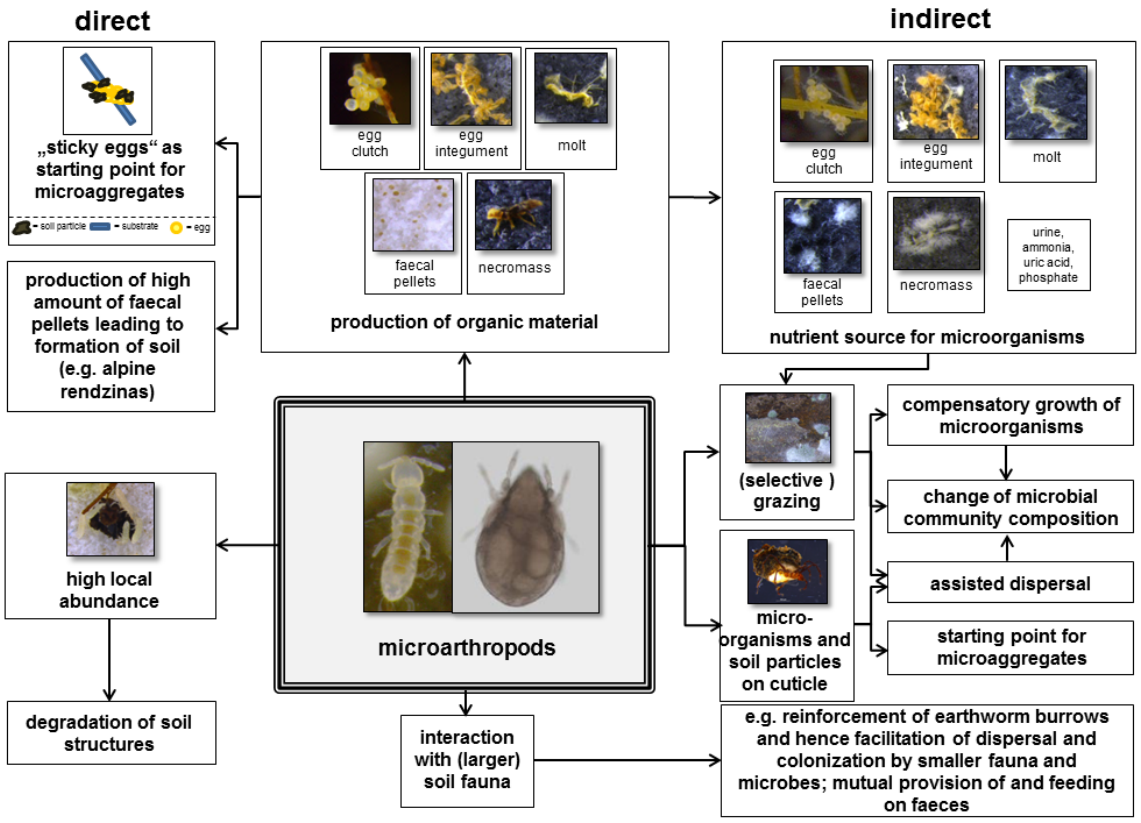

Fig. 3.1 Overview of potential mechanisms used by microarthropods for the formation of soil aggregates. Mechanisms are divided into direct and indirect processes and basedon Collembola and oribatid mites as most abundant soil microarthropod representatives.

Direct mechanisms

Direct effects of collembolans on soil structure can be categorized in terms of input of organic material, which positively contributes to soil structure, and degradation of aggregates, which is a negative effect.

Organic matter inputs

Possible positive, direct effects of collembolans on soil structure include the production, modification and movement of organic matter, which can then serve as binding agents, nuclei or building blocks for aggregates. Assimilated nutrients can either be contained in animal tissue or be excreted as metabolic waste. Especially because microarthropods can occur in high numbers, they might produce a large amount of fecal pellets. It has to be assumed that many soils contain millions of fecal pellets per square meter (Hopkin, 2007). In this context, Kubiena (1953) reports about the so-called ‘alpine pitch rendzinas’ on limestone which are nearly completely composed of collembolan feces forming a 15–20 cm deep black humus layer.

Collembolan eggs are deposited in clutches and need a couple of days to weeks to develop (Hopkin, 2007). Eggs of the collembolan family Sminthuridae might be covered by a mixture of soil and collembolan waste to protect them from mold and dehydration (Betsch-Pinot, 1976, Betsch-Pinot, 1977 and Dallai et al., 2008). After hatching, the remaining egg integuments might serve as source of fresh organic material to microorganisms (which will be discussed in the paragraph about indirect mechanisms) or, due to the attached soil particles and organic material, as nuclei for microaggregate formation. Collembolans go through several instars, which might mean molting at fairly high rates. Most species molt throughout their whole life (up to 45 times). Specimens of *Folsomia candida* may live up to six months; however, for other species shorter or far longer (one year and longer) life-spans have been reported (Hopkin, 2007), which means that their production of molts could be significant. Interestingly, some oribatid mites can even survive for up to three years (Capinera, 2008). Their molts are hard-bodied due to chitin and other components in the cuticle (see Weigmann, 2006) and hence their breakdown should be slower, and thus they could serve as more long-lived building blocks of aggregates. Finally, the production of necromass especially in short-lived species besides fecal pellets, molts and eggs, can potentially influence soil aggregation. Unfortunately, there is no study dealing explicitly with the input of these types of organic material. Given the potentially high local abundances, this should clearly be a target of future research.

Degradation of soil aggregates via disturbance

Collembola and Oribatida usually consist of populations in the order of 10,000–100,000 individuals per square meter (see Weigmann, 2006 and Hopkin, 2007). Can they therefore counteract the formation of aggregates by crawling around or feeding on e.g. microorganisms, plant remains or various excretory products? The impact of this disturbance on a *per capita* basis might be low, but data about the impact of locally highly abundant microarthropods on soil aggregation are missing.

Indirect mechanisms

Several studies have investigated the soil food web, functional characteristics and feedbacks between the different organism groups also in relation to aboveground biota; however, there are few data on the impact of interacting taxa like fungi and microarthropods on soil aggregation (Salmon and Ponge, 2001, Siddiky et al., 2012a and Siddiky et al., 2012b). Fungi and bacteria are directly and indirectly contributing to the production and release of materials and compounds that contribute to soil structure dynamics while soil animals affect the translocation and provision of organic material for colonization, like fecal pellets, molts, eggs, and necromass, and the modification of the activity of microorganisms by grazing (Coleman et al., 2002). There are studies suggesting that Collembola could have a positive

effect on mycorrhizal functioning as their fungal grazing might enhance fungal growth and respiration (Lussenhop, 1992). Other studies suggest that collembolans could also have no or negative effects (Fitter and Sanders, 1992 and Fitter and Garbaye, 1994), which brought attention to collembolans as important regulators of the mycorrhizal symbiosis acting in a density-dependent fashion (Gange, 2000). If there were positive effects on fungal growth or branching patterns, these effects could enhance soil aggregation processes, while the reduction of fungal biomass could have either negative effects or change the composition of the soil microbial community with unclear functional consequences. It is also likely that the observed effects depend on the abundance of Collembola or other microarthropods, a hypothesis that should therefore be tested (for enchytraeids see Hedlund and Augustsson, 1995). It has also been shown that Collembola do feed on arbuscular mycorrhizal fungi (AMF), but, depending on the species, prefer non-AMF mycelia (e.g. Moore et al., 1985, Thimm and Larink, 1995, Klironomos and Kendrick, 1996 and Klironomos and Ursic, 1998). Another important aspect of the interaction between the microbial community and microarthropods is the dispersal of spores (Lussenhop, 1992 and Klironomos and Moutoglis, 1999). AMF spores can be far larger (20–500 μm) than non-AMF spores (Trappe, 1982) and it is more likely that spores are ingested by earthworms rather than by Collembola (Moore et al., 1985 and Fitter and Sanders, 1992). Brown (1995) has shown that spores can survive the gut passage of earthworms with an increased germination rate afterwards (for more information about gut microbiota in various taxa see e.g. Pherson and Beattie, 1979, Ponge and Charpentié, 1981 and König, 2006). Still, collembolans are also able to act as vectors by transporting spores attached to their cuticle (Gormsen et al., 2004), which is also known for one oribatid group, the Damaeidae (Weigmann, 2006). Although this phenomenon might be restricted to only a few species it should be considered as important means of microbial transport which might have an impact on the composition of the microbial community.

As described in the paragraph about the provision of organic material, one major question is how the organic materials influence the colonization by and composition of microbial communities, which might lead to enhanced aggregate formation. There are several potential mechanisms which have been investigated only in part so far.

Foster et al. (1983) report that fresh fecal pellets can be recognized as round and smooth surfaces under the scanning electron microscope, whereas older pellets are mostly densely covered by fungal hyphae; this highlights the importance of microarthropods in assisting microbial colonization of organic matter. It is also known that during the molting of collembolans the whole midgut epithelium is also excreted to dispose of the accumulated toxins (Humbert, 1997 and Fountain and Hopkin, 2001). The total gut volume of *Folsomia candida* was estimated up to 10 nl, fecal pellets had a volume of approx. 1 nl (Thimm et al., 1998) and contained approx. 1.55 × 104 bacterial cells (identified by light microscopy) of which only less than 0.01% were dead. Taking into consideration that, under laboratory conditions, the reported period between the ingestion and the defecation of bacterial cells

can be less than one hour (Czarnetzki and Tebbe, 2004), the amount of living microbial cells excreted per individuum during a life cycle is enormous. Some authors (e.g. Hanlon, 1981 and Thimm et al., 1998) have already highlighted the importance of the constant local input of gut (but also other ingested) bacteria which might lead to an enhanced competition between already existing soil microorganisms, and this might affect soil aggregation depending on the ensuing species composition. The same might also be true for other organic material provided through oviposition or necromass.

Collembolans usually excrete urine via the labial nephridia, but can also release insoluble products via the midgut epithelium (Hopkin, 1997 and Larsen, 2007). Most of the nitrogenous and phosphorus-containing waste products are released as ammonia (Sjursen and Holmstrup, 2004), uric acid and phosphate, depending on the species. In spite of the studies addressing these aspects (e.g. Verhoef et al., 1988, Cragg and Bardgett, 2001 and Milcu et al., 2006) it is not clear how these different waste products influence local environmental conditions and hence the microbial community. Some studies have also investigated partly species-specific characteristics of nitrogen and carbon release (Petersen, 1980 and Sjursen and Holmstrup, 2004), the influence of the available resource quality (Chen et al., 1995) and the creation of nutrient sources for heterotrophic microbes and primary producers (Rusek, 1998). These processes should therefore be recognized as integral components of soil structure (Rusek, 1985 and Fjellberg, 1986).

Indirect effects of microarthropods via the provision of organic material to microorganisms are not the only indirect mechanisms to be considered. The complex interactions with the larger components of the soil fauna have not yet been considered in detail in any study (but see Ponge, 1988, Ponge, 1991 and Salmon and Ponge, 2001). In our opinion, especially the interaction between different functional groups should be more closely investigated, as the biggest effect sizes are assumed to be found in this context rather than in studies dealing with direct effects.

Another important aspect is the impact of different agricultural practices on soil fauna and soil aggregation as abiotic factors. Once the biotic interactions between different faunal groups have become clearer, another focus should be on the impact of tillage, ploughing or compaction of soil on these interactions. It is known that different taxonomic groups respond differently to agricultural practices in different types of soils and depending on fertilizer additions etc. (see e.g. Roger-Estrade et al., 2010 and Van Cappelle et al., 2012, for microarthropods see Ponge et al. 2013), however, closer investigation would be necessary in order to develop appropriate strategies to e.g. increase soil fertility and resistance toward erosional loss by increasing soil stability via soil fauna.

Conclusion

Despite their underrepresentation in the soil aggregation literature, we highlighted and discussed several potential mechanisms via which microarthropods could influence soil aggregation.

Due to their relatively small body size and total biomass, which is lower than that of fungi, bacteria and other taxa such as nematodes and protozoa, microarthropods may rather indirectly than directly affect soil structure. However, in some cases the impact of the production of assumedly large amounts of organic material in form of necromass, eggs, etc. might play an important role as direct starting points for microaggregate formation. We propose to start studying soil aggregation formation with easy-to-handle species such as *Folsomia candida* in experimental designs that allow assessing the direction and magnitude of the various possible mechanisms, especially direct vs indirect mechanisms. Difficulties with culturing microarthropods for experiments, but also with the collection of direct observations have hampered empirical studies to date. The usage of high resolution filming and photographing, which is nowadays very feasible given the remarkable advances in microscopy technologies, is necessary to observe how microarthropods act in the formation of soil aggregates. Coupling these technologies with small scale experimental designs will allow teasing apart the roles of various mechanisms that act simultaneously. An element of complexity and realisms will be given by studies addressing the impact of different taxa (e.g. Collembola and Acari) on soil structure in opposition to studies focusing on species-specific effects. In this context, a focus should in our opinion be on the interaction of functionally defined, trait-based groups across all soil biota.

Acknowledgement

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4 Disturbance, neutral theory and patterns of beta diversity in soil communities: the example of oribatid mites

Abstract

Beta diversity describes how local communities within an area or region differ in species composition/abundance. There have been attempts to use changes in beta diversity as a biotic indicator of disturbance, but lack of theory and methodological caveats have hampered progress. We here propose that the neutral theory of biodiversity plus the definition of beta diversity as the total variance of a community matrix provide a suitable, novel, starting point for ecological applications. Observed levels of beta diversity (BD) can be compared to neutral predictions with three possible outcomes: Observed BD equals neutral prediction or is larger (divergence) or smaller (convergence) than the neutral prediction. Disturbance might lead to either divergence or convergence, depending on type and strength. We here apply these ideas to datasets collected on oribatid mites (a key, very diverse soil taxon) under several regimes of disturbances. When disturbance is expected to increase the heterogeneity of soil spatial properties or the sampling strategy encompassed a range of diverging environmental conditions, we observed diverging assemblages. On the contrary, we observed patterns consistent with neutrality when disturbance could determine homogenization of soil properties in space or the sampling strategy encompassed fairly homogeneous areas. With our method, spatial and temporal changes in beta diversity can be directly and easily monitored to detect significant changes in community dynamics, although the method itself cannot inform on underlying mechanisms. However, human-driven disturbances and the spatial scales at which they operate are usually known. In this case, our approach allows the formulation of testable predictions in terms of expected changes in beta diversity, thereby offering a promising monitoring tool.

Introduction

Ecological communities are not homogenous in space and time for a number of reasons: dispersal processes, stochastic demographic fluctuations, environmental filtering, niche partitioning processes, and biotic interactions within and between trophic levels interact to determine variable patterns of covariation in species distribution (Hubbell 2001; Chase and Leibold 2003; Morin 2011; HilleRisLambers *et al.*2012). Disturbance is one of the processes that contribute to the spatial and temporal heterogeneity of communities (Walker 2012): If communities are equilibrium assemblages of coexisting species (Chase and Leibold 2003; Morin 2011), disturbance prevents assemblages from reaching the equilibrium state. This process can create a long-lasting state of nonequilibrium conditions that promote diversity (e.g., the intermediate disturbance hypothesis; Connell 1978). Communities can also be governed by processes such as chaotic dynamics (May 1973; Morin 2011)

where populations are regulated by deterministic factors but are very sensitive to initial conditions: Even the smallest change in the initial state leads to strongly diverging temporal trajectories of population densities. In this case, disturbance can affect initial conditions (e.g., the initial abundance of certain species) by continually resetting them, thereby contributing to rendering the assembly process highly uncertain and variable in terms of the species that locally come together to form assemblages. Communities could also be assembled purely through stochastic processes such as those assumed in neutral theories (Bell 2001; Hubbell 2001). In this latter set of theories, processes such as niche partitioning are just ignored when predicting basic community properties such as variation in species richness or species spatial turnover (Condit *et al.*2002). In this case, disturbance can take the form of, for example, increased habitat fragmentation, which is expected to reduce dispersal, thereby increasing beta diversity.

Recently, ecologists have become interested in the effects of disturbance on the spatial distribution of coexisting species. Metacommunity frameworks (Leibold *et al.*2004) are useful as they consider a set of local communities embedded in a landscape and connected by dispersal processes within a matrix that might experience heterogeneous conditions, for example, but not only, in terms of environmental gradients. In this framework, local communities are assembled under different forces, and different assembly processes (species sorting, mass effects, and patch dynamics) can be described depending on the relative effects of these forces, which interact as follows: The environment locally filters dispersing species, which might interact with each other under niche partitioning processes but can also be supported by immigration if dispersal rates are adequate. Disturbance might alter these processes either via affecting dispersal (e.g., isolation of patches via habitat fragmentation) or via increasing spatial heterogeneity in environmental conditions, or both. These two effects of disturbance can take place at different scales, as in the case of soil communities (Ettema and Wardle 2002): In soil, local communities can be defined at very fine scales such as the rhizosphere of a single plant. Also, steep gradients in variables such as pH, oxygen, and nutrients are observable already over a few centimeters (Bardgett 2005). At larger scales, such as those relevant to fire or agricultural practices such as tillage, disturbance can either increase or decrease environmental heterogeneity. For example, in the case of high-temperature fire, the intensity of disturbance is patchily distributed, increasing environmental heterogeneity within the extent of the fire. On the other hand, agriculture is a homogenizing disturbance that mixes up soil vertically while it horizontally reduces the diversity of organic input, patchiness, or gradients in the distribution of nutrients: For example, the establishment of monocultures represents an homogenizing environmental factor at a landscape scale (Wardle 2002; Bardgett 2005; Walker 2012).

If spatial heterogeneity determines heterogeneity in the composition of local assemblages, we also expect disturbance to increase beta diversity if it also increases environmental heterogeneity (Dornelas *et al* 2006; Caruso *et al.* 2012a,b). For the same principle and on the other hand, if disturbance

homogenizes spatial properties, we expect a decrease in beta diversity. In this sense, very different mechanisms such as a neutral assembly processes versus niche assembly processes (as well as other processes discussed above) can lead to the same pattern given the factor causing the pattern (disturbance). This offers high potential for applications such as environmental monitoring and conservation (Anderson *et al.* 2006, 2011; Dornelas *et al.* 2006; Caruso *et al.* 2012a,b) because disturbance is expected to cause recurrent patterns in beta diversity, regardless of the mechanisms governing the assembly process. Thus, the simplest set of processes (e.g., neutral dynamics) can offer a baseline to detect disturbance, as we argue below.

However, two problems potentially hamper applications: First, beta diversity has proved to be a multifaceted and even controversial concept (Legendre *et al.* 2005; Tuomisto and Ruokolainen 2006; Anderson *et al.* 2011; Legendre and De Cáceres 2013); second, testing for differences in beta diversity is complicated by the numerous ways in which beta diversity can be measured, and the statistical and dynamical (sensu community dynamics) links between beta diversity and gamma diversity (Kraft *et al.* 2011; Legendre and De Cáceres 2013; Myers *et al.* 2013).

We here propose two solutions, based on some of the ideas that have been recently discussed in the field: (1) We apply the recent definition of beta diversity as total variance of the community matrix (Legendre and De Cáceres 2013); (2) we use a general neutral model to create a null prediction of beta diversity under the simplest metacommunity scenario (Dornelas *et al.* 2006; Etienne 2007; Gotelli and Ulrich 2012). There are several advantages to this approach. Beta diversity is summarized in one number that is easy to calculate and interpret. Most importantly, this number is not computed from alpha and gamma diversity while its statistical dependency on gamma and alpha diversity (Kraft *et al.* 2011) is taken into account through the use of a general neutral model. We here use such a model to produce a statistical null distribution of beta diversity based on fundamentals of population dynamics (Rosindell *et al.* 2012). Observed beta diversity can be compared to this distribution (Fig. 4.1).

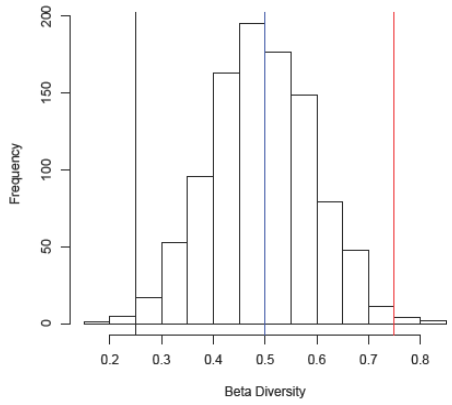

Fig. 4.1 This conceptual figure shows the qualitative idea behind the method applied in this study: The beta diversity of a real set of local assemblages (lines) can be similar to (blue line), higher than (red line), or smaller than (black line) the mean of a distribution of beta diversity values obtained from a neutral model. Neutral models assume simple population dynamics that provide background levels of beta diversity, with a mean and a variance. However, real dynamics, based on processes such as environmental filtering, can make real communities significantly diverge (red line) or converge (black line) relative to their neutral counterpart.

Here we test this approach on our own datasets that describe soil oribatid mites under several disturbance regimes and a range of natural, undisturbed environments. Oribatid mites together with collembolans represent the most diverse and abundant group of soil microarthropods: These mites play a key role in soil organic matter decomposition (Scheu 2002; Bardgett 2005; Maraun *et al.* 2011; Caruso *et al.* 2012b) and have been studied extensively with regard to both testing general assembly models in soil assemblages (Anderson 1975; Lindo and Winchester 2009; Nielsen *et al.* 2010; Caruso *et al.* 2012b) and investigating the response of soil animals to human activities (Behan-Pelletier 1999; Caruso *et al.* 2008; Al-Assiuty *et al.* 2014). Soil assemblages possess interesting metacommunity properties: They are assembled at multiple spatial scales, and several species have limited dispersal capability (Ettema and Wardle 2002). For this reason, the assembly of taxa such as oribatid mites has been studied in the framework of the debate around neutral theories (Lindo and Winchester 2009; Caruso *et al.* 2012b). We here quantify the beta diversity of oribatid mite assemblages under several types and regimes of disturbance and natural environmental heterogeneity. Given mechanisms that were already known to be likely to operate, these different disturbances or conditions were expected to produce variable levels of beta diversity that, depending on disturbance type and/or environmental conditions, could be lower than, higher than, or consistent with beta diversity levels predicted by a general neutral model. We here also provide our original R scripts and relevant data to show how to apply the method, and we discuss how results may inform about ecological applications, in particular the monitoring of communities subjected to disturbance regimes.

Material and Methods

Our original aim was to use results from a literature search using the Web of Science and the following key words: oribatid*, abundance, distribution* pattern*, soil, community, structure* (in various combinations). We wanted to include all studies on European oribatid soil fauna in nonextreme habitats since 1950. Unfortunately, after this search, at least as to August 2013, only very few studies reported the species abundance table that is necessary to fit neutral models, and very often, these few studies reported data for a low number of replicates. We therefore decided to base our analysis on our own datasets, one of which is unpublished while the others were the subject, to different extents, of previous publications (Migliorini *et al.* 2002; Caruso *et al.* 2005, 2009; Caruso and Migliorini 2006). Eventually we were able to compile twelve datasets: Six of them were obtained from undisturbed areas (a beech forest, two grasslands, the thin, rocky, undifferentiated soils of two arid Mediterranean islands, the control plot of a Mediterranean maquis subjected to experimental fires), the other six datasets were obtained from metal-polluted soils, experimentally burned plots, coppice, a badland and heathland resulting from agriculture activities. In the case of metal-polluted soils, the pollution gradient was very steep already at small scales (Caruso *et al.* 2009), and we could expect diverging assemblages in this case. Even moderate fires usually cause very patchy disturbance regimes, due to the irregular distribution of fire intensity (Caruso and Migliorini 2006), and therefore, we expected diverging assemblages also in this case, and both within and between plots. In the case of land management, we could expect either converging assemblages (i.e., homogenized assemblages) given the scale at which we sampled or diverging assemblages depending on the land use.

The species abundance distribution of each sample (i.e., the local community) was used to estimate the two main parameters of neutral theory: theta (θ), an index of diversity, and immigration rate (I). We used the formula for multiple samples by (Etienne 2007) to estimate neutral parameters using the PARI/GP codes given in Etienne (2007). With the estimated parameters, we used the Pari/GP function urn2.gp (Etienne 2007) to create 4999 neutral equivalents of each dataset, which eventually allowed us to create a null distribution of beta diversity for each dataset. For the estimate of neutral parameters and the function urn2.gp, see Data C.S1. The output of this analysis is the input for the R script reported in Data C.S2. Beta diversity (BD) was quantified using the approaches proposed by Legendre and De Cáceres (2013). These authors propose to quantify beta diversity as the sum of species variances in the species by site matrix (see Data C.S1 for a full definition), the latter matrix being the typical outcome of community studies. As this definition of beta diversity implies that the ecological dissimilarity between sites is Euclidean, data must be properly transformed to be ecologically meaningful. Alternatively, meaningful ecological distance matrices can be computed from the raw data and used to estimate BD. This is the most important, central aspect and advantage of this definition of BD, which makes beta diversity a quantitative measure capable of capturing the variation described in the past through a multitude of often redundant dissimilarity indices (see also table 1 in

Legendre and De Cáceres (2013). The metric proposed by Legendre and De Cáceres (2013) seems particularly useful because it fits well into two main aspects of neutral models: Spatial changes in species composition are due to dispersal processes, and the variance in species abundance is caused by stochastic demographic fluctuations.

Table 4.1 Characteristics of the twelve assemblages tested. Bold effect sizes were significant at $P \leq 0.05$ (see Fig. 4.2).

Study[a]	N[b]	Habitat	Spatial scale	Beta diversity factors	Effect size[c]
S1a	10	Beech forest stand	20 x 20 m plot	Natural, undisturbed area	1.04
S1b	10	Grass stand	20 x 20 m plot	Natural, undisturbed area	0.89
S1c	10	Coppice stand	20 x 20 m plot	Disturbed by cutting	**1.70**
S1d	10	Heathland	20 x 20 m plot	Heterogeneous	**1.99**
S1e	10	Badland	20 x 20 m plot	Homogeneous, dry	0.92
S2	36	Dry Grassland	15 x 15 m plot	Natural, undisturbed	-0.79
S3a	22	Lampedusa Is., rocky soil	20 km^2	Very heterogeneous	**2.49**
S3b	10	Linosa Is., rocky soil	150 m transect	Elevational gradient	**4.36**
S4	24	Grass stand	10 x 40 m plot	Metal pollution	-0.42
S5a	9	Mediterranean Maquis	Three 10 x 5 m plots	Control experiemental fire	**1.51**
S5b	9	Mediterranean Maquis	Three 10 x 5 m plots	High-intensity fire	**2.25**
S5c	9	Mediterranean Maquis	Three 10 x 5 m plots	Low-intensity fire	0.15

[a]References for major details on the study areas and methods: S1, Migliorini et al. 2002; S2, unpublished, see methods; S3, Caruso et al. 2005; S4, Caruso et al. 2009; S5, Caruso and Migliorini 2006.
[b]N is the number of local communities (independent soil samples).
[c]Effect size was equal to [BD-Mean (simulated BDs)]/standard deviation (simulated BDs), BD being beta diversity and simulated BDs being the distribution of BDs obtained for each of the 4999 simulated neutral communities (Fig. 4.2).

There are many options for both data transformation and distance matrices (Legendre and De Cáceres 2013). We here apply the Hellinger transformation, which has several advantages (Legendre and De Cáceres 2013): (1) The relevant Euclidean distance matrix can be analyzed by principal component analysis (PCA) or canonical redundancy analysis (RDA); (2) the calculation of BD on raw data after transformation is straightforward; (3) BD ranges from 0 to 1; and (4) Hellinger transformation allows to calculate the 'species contribution to beta diversity' statistics. Additionally, the Hellinger transformation does not inflate the weights of rare species (Legendre and Gallagher 2001).

BD was calculated using the R function provided in Legendre and De Cáceres (2013). This statistic was calculated on the real datasets, and each of the 4999 neutral datasets simulated for each dataset. If the observed BD was higher or lower than 95% of the simulated datasets, the observed (real) community was considered to have respectively higher or lower beta diversity than expected under neutral assembly (Fig. 4.1). Otherwise, data were consistent with neutral dynamics. Given the regime of disturbance or degree of environmental heterogeneity was known for each dataset, results could be interpreted in terms of expected dynamics and outcomes.

Results

Six of twelve datasets had beta diversity (BD) significantly higher (Fig. 4.2, see red line) than the null distribution obtained by calculating BD on the 4999 datasets generated with the neutral model of Etienne (2007). These datasets were S1c (Coppice), S1d (Heathland), S3a and S3b (Lampedusa and Linosa), S5a (Control Fire Experiment), and S5b (High-intensity Fire). The effect sizes reported in Table 1 were in these cases significant at $P \leq 0.05$, meaning that less than 5% of simulated BDs were larger than the observed BD. In the other six cases, the effect size was not significant: In two of these cases, the Dry Grassland and the Metal polluted plots observed BD was smaller than the mean of simulated BDs, while in the remaining four cases, observed BD was larger.

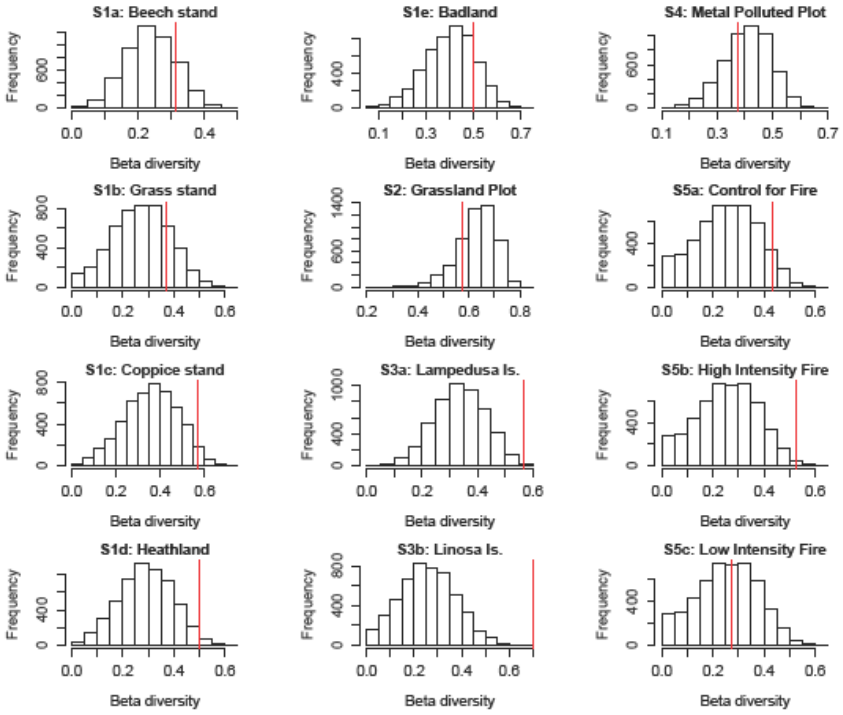

Fig. 4.2 The observed beta diversity (red line) is compared to the frequency distribution of 4999 beta diversity values obtained from simulated neutral communities. Beta diversity is computed as the total community variance of the Hellinger transformed species by sites abundance table (Legendre and De Cáceres 2013; Data C.S1). The parameters used to simulate neutral communities were estimated from the real data using Etienne (2007).

Discussion

Disturbance generally is detrimental to soil biodiversity (Walker 2012; Ponge and Salmon 2013), especially in agroecosystems, where it is usually intense and frequent. In fact, the spatial homogenization caused by activities such as tillage reduces biological diversity in space and time: A few species eventually dominate the system. On the other hand, natural soils are highly heterogeneous at multiple spatial scales (Ettema and Wardle 2002) and already over a few centimeters (Wardle 2002; Bardgett 2005), and certain regimes of disturbance can actually increase spatial heterogeneity (Walker

2012). Accordingly, several soil taxa are characterized by high species turnover and variance in abundance, that is to say high beta diversity (Lindo and Winchester 2009; Caruso *et al.* 2012b; Ponge and Salmon 2013). Here we show that six of the twelve tested oribatid mite assemblages diverge relative to the reference point provided by a general neutral model. If we assume that background levels of beta diversity depend on the basic processes postulated by neutral theories (dispersal and stochastic demographic fluctuations), our result means that real communities have higher beta diversity than expected under neutral dynamics. Note that this fact does not imply that communities consistent with neutrality have low beta diversity.

In the other six cases, beta diversity was consistent with neutral predictions. When neutral models are used to build a null distribution and data do not reject the null hypothesis (Rosindell *et al.* 2012), nothing certain can actually be said on underlying mechanisms (Gotelli and Ulrich 2012). Communities could be neutrally assembled, but possible issues of statistical power or inadequate sampling strategy could also be invoked to explain the results.

Whatever the actual mechanism, the main point of our results is that there is a clear qualitative, simple explanation of why certain assemblages diverge relative to neutral predictions: When disturbance is expected to increase the heterogeneity of soil spatial properties or the sampling strategy encompassed a range of diverging environmental conditions, we observed diverging assemblages. On the contrary, we observed patterns consistent with neutrality when disturbance could determine homogenization of soil properties in space or the sampling strategy encompassed fairly homogeneous areas. Etienne (2007) suggested that one of the reasons why currently available general neutral models might fail in terms of predicting beta diversity is that these models are spatially implicit, even when they allow estimating single dispersal rates for each local assemblage. Disturbance and/or environmental heterogeneity can therefore contribute to the failure of neutral models via affecting assemblages selectively in space, with closer localities that are subject to similar disturbance intensity and frequency. In this sense, it is interesting to pinpoint specific results from disturbed or undisturbed areas that were consistent with neutral expectations. The metal-polluted plot and low-intensity fire, for example, were consistent with neutral predictions. The metal-polluted plot (Caruso *et al.* 2009) was 40 × 10 m, and within this area, basic soil parameters (e.g., water content, pH, C) and vegetation were fairly homogenous. Metals such as Pb, Zn, and Cu did show steep gradients over 40 m, but we had previously shown that these gradients did not correlate with oribatid mite distribution after removing spatial autocorrelation (Caruso *et al.* 2009). The collected local assemblages can therefore be seen as random variation around the same core assemblage, which might explain the consistency between neutral predictions of beta diversity and observed beta diversity. The same applies to the data obtained from a 15 × 15 m plot in a dry grassland plot. In theory, one direction of the plot was aligned with an environmental gradient, and assemblages might therefore be expected to diverge. In practice, assemblages did not diverge significantly relative to a neutral model, and we hypothesize that this

depends on the small scale of the sampling, not sufficient to encompass the environmental divergence that could make local assemblages significantly diverge. On the other hand, we could have observed convergence: The environment is fairly homogeneous, and the assemblage should therefore converge to the equilibrium expected for the given environmental condition. The observed negative effect size (Table 1) indicated some degree of convergence, but the difference was not statistically significant. Issue of statistical power may apply to this case. The same issue possibly applies to data collected in natural beech and grass stands which were not disturbed: Also in these two cases, the spatial scale of the sampling was relatively small although larger than that of the dry grassland plot. In this case, the effect size indicated some degree of divergence, but again results were not significant (Table 4.1).

We can therefore understand the nonrejection of neutral models in terms of either the sampling scale of the study and/or statistical power. This seems reinforced by the cases where we did observe significant divergences: In coppice and heathland that were sampled at the same scale as the beech and grass stands, we did observe significant divergence, which is consistent with the high heterogeneity associated with the tree harvests and the management of heathland. The divergence observed in the extremely dry, thin, and rocky soil of Lampedusa (different habitat types sampled within the island; see Caruso *et al.* 2005) and Linosa (a transect along an elevational gradient) islands can be interpreted in a similar way: In this case, the sampling strategy aimed at maximizing environmental gradients and heterogeneity.

An interesting set of comparisons is that of the three assemblages from the fire experiments: The control assemblages show beta diversity higher than the neutral prediction. The low-intensity fire communities were consistent with the neutral model. The high-intensity fire resulted in beta diversity much higher than the neutral prediction (compare the three effect sizes in Table 4.1 and Fig. 4.2). Relative to low fire intensity, high-intensity fire produced a very patchy disturbance with patches that were much more intensely burned than other patches (personal observation): We attribute the observed differences to this effect.

Overall, the results support the general hypothesis that neutral models allow detecting changes in beta diversity caused by disturbance regimes that increase environmental heterogeneity or by natural environmental heterogeneity, which is usually captured at broad scales (>100 m; e.g., Lampedusa and Linosa, Table 4.1).

There are technical aspects relevant to our interpretation of results and possible applications that are avenue for future research. Neutral models provide a robust null hypothesis because they can provide estimates of beta diversity based on the simplest metacommunity scenario. However, neutral models can be used to detect disturbances in two different ways: First, data reject neutral predictions because the real assemblages vary too much or too little in terms of species composition and abundance (Dornelas *et al.* 2006; Caruso *et al.* 2012a,b); second, communities are really assembled under neutral

dynamics, and disturbance directly affects neutral parameters, for example, by decreasing dispersal via increasing habitat fragmentation (Hubbell 2001) or by affecting some fundamental demographic parameters (Dornelas 2010). In this study, we basically used neutral models in the first sense because we believe that in observational studies, robust conclusions can be obtained only when sound statistical null hypotheses are rejected (Gotelli and Ulrich 2012). We also believe that in the framework of observational studies, our modeling approach does not allow identifying mechanisms but rather monitoring changes given expectations that come from background knowledge on the study area.

We use a quantitative definition of beta diversity, but one can further simplify the concept by focusing just on compositional aspects, which is done using indices such as the Jaccard index. In this case, community variance (Legendre and De Cáceres 2013) would reflect just changes in species composition across the study area.

In this sense, an interesting aspect to be investigated is the partitioning of beta diversity in terms of pure compositional variation and pure variance in species abundance, a topic that, as far as we are aware, has been introduced in the seminal paper by Anderson *et al.* (2006) but never analyzed in terms of applications. Ecologically, these two aspects can imply fairly diverse scenarios. Local assemblages can be very different in terms of species composition even if the spatial variance of each species is low and vice versa. In theory, a set of local assemblages can have zero BD if the assemblages are identical in terms of species composition and BD is measured using presence/absence data. However, species abundance usually has some associated variance, and if BD is measured using metrics that take into account quantitative information, BD will not be zero. A key aspect of many definitions of disturbance is that disturbance implies some change in the biomass or abundance of the disturbed population (Walker 2012). This suggests that, especially for applications relevant to the monitoring of the effects of human-induced disturbance, a quantitative approach to BD is worth using to increase our ability to detect effects and eventually interpret them. Theoretical studies based on simulations and accompanied by relevant field experiments are the tools to validate this method in the future. In the meantime, we propose to monitor the effect of disturbance on community structure and the effect of restoration practices using the following seven steps procedure: (1) Assess whether the disturbance regime under investigation increases or decreases environmental heterogeneity and/or environmental predictability and fragmentation; (2) sample local communities at the range of scales pertinent to the disturbance regime; (3) estimate beta diversity using the metrics proposed by Legendre and De Cáceres (2013); (4) fit a general neutral model to species abundance data in order to create a null prediction of beta diversity (Etienne 2007; Data S1); (5) use the null distribution to assess whether the sampled assemblages are diverging or converging relative to their theoretical neutral counterpart, or the assemblages could be consistent with the neutral model (Data S2); (6) assess: if the assemblages are diverging under a disturbance regime that increases heterogeneity or converging under a disturbance

regime that homogenizes the environment, then the conclusion is that disturbance is deeply affecting community dynamics with effects on species abundance and composition; (7) plan of action: arrange for replicating observations of the disturbed community in time, also in connection with restoration regimes. If beta diversity is quantified using BD by Legendre and De Cáceres (2013) on Hellinger transformed data, species most responsible for changes in beta diversity can be identified.

Acknowledgments

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5 General Discussion

There are various processes which influence community structure on multiple scales: environmental filtering, dispersal and biotic interactions but also niche partitioning and stochastic demographic fluctuations. These structuring forces act not only within but also across trophic levels and hence result in various observable patterns of covariation of species distribution (Hubbell 2001, Chase & Leibold 2003, Morin 2011, HilleRisLambers *et al*. 2012). 'The niche' is an 'easy to grab' and plausible core ecological concept and has been used as a generic assumption in ecology (McGill *et al.* 2006, Newsome *et al.* 2007) for decades until it was challenged by upcoming neutral viewpoints (most famously Hubbell 2001). Although these two theoretical approaches seem to be exclusive on the first glance and have launched an ongoing discussion about which approach fits the data better (Chave 2004), ecologists now have started to fuse the respective assumptions (Tilman 2004, Alonso *et al.* 2006, Adler *et al.* 2007, Purves & Turnbull 2010, Caruso *et al.* 2012a,b). One influential development has been that neutral models have been recognized as useful tool in terms of being a null model to test for niche based assumptions. In this thesis, we will make use of the various theoretical, methodological and statistical approaches to quantify the roles of niche and neutral based factors which influence structures of soil microarthropod communities.

What would we have expected under the respective viewpoints? In the niche framework, we would have expected to see a significant influence of the environment on the community structure which would result in a species turnover along the environmental gradient encompassed by our sampling design. Under the neutral perspective, space and hence dispersal, would display the major explanatory power for community structure. Finally, we expected to see evidence for another core concept in niche based theories, the limiting similarity concept, which could have appeared in form of resource partitioning, size differences or significant differences in the depth distribution of potentially competing species which could also create spatial patterns. Especially competition for the exploitation of resources is assumed to be of utmost importance (Hairston *et al*. 1960, Scheu & Setälä 2002) which is why we will discuss our results in this respect in detail. The results we present in chapter 2 were surprising but we will show in the following discussion that they create very interesting findings about the oribatid mite community of a dry grassland in Brandenburg, Germany.

Niche based processes

For accounting for the major environmental factors, we measured water content, pH, content of C and N as well as soil structure. A Variance Partitioning analysis revealed, that 1% of community variance can be accounted for by pure environmental factors, whereas 21% were accounted by spatially structured and 10% by pure spatial variables while 68% remain unexplained. In a PCA of the

environmental variables, organic matter content (i.e. content of C and N) and soil structure were the major predictors for community variance, followed by a negative covariation between water content and C:N ratio. The first two axes described 77% of the total variance which illustrates the effect of environmental factors on the oribatid community and hence supports the expectations of niche based theories and the validity of our sampling design. There are countless examples in the literature of the last decades which have shown the strong correlation of species with one or several of the mentioned factors. In our analysis we also observe a spatially structured correlation between the environmental gradient and the community structure which is evidence for environmental filtering. However, this does not imply that resource –based niche partitioning processes are happening which can be explained by both, niche and neutral based viewpoints (Hubbell 2005, HilleRisLambers *et al.* 2012). In chapter 2, this issue is discussed in detail. For gaining evidence for niche partitioning, we included the stable isotope signatures (^{13}C and ^{15}N), body size and depth distribution of the respective species into our analysis as most probable traits involved in trade-offs (for chilopodes see Poser 1988, Ferlian & Scheu 2014). This is based on the classical concept of limiting similarity: if niche partitioning is happening, we should see a trade-off (e.g. in terms of body size or spatial segregation) between species which are close in space and time when competing for resources. The latter part of this assumption is a rather important point which has been overlooked until now: niche and neutral based theories should be applied to one trophic level only to ensure to include species which are actually competing for the same resource. This might have strong implications on the outcome of the analyses. We therefore focus on our analyses on the group of fungal feeders which include most of the species of the assemblage based on stable isotope analysis (but compare Chapter 2 and Appendix Fig. B S2 for details).

Interestingly, in contrast to our expectations, size did not reveal evidence for niche partitioning. Still, size should always be taken into account at least in the very first analyses, as, although seemingly not in our study, size has been shown to be an important factor which influences the distribution of species and hence competition (Hutchinson 1959, Woodward & Hildrew 2002, Brose *et al.* 2005, Kalinkat *et al.* 2015). In this community, species are mostly on the lower end of size range boundaries described in e.g. Weigmann (2006) (compare Table A S1). We can only speculate why this is the case, however, morphological plasticity as adaption to local conditions (environmental filtering) has been shown for e.g. *Oppiella nova* (von Saltzwedel *et al.* 2014), a species which is also present in this community. Harsh environmental conditions might have led to filtering for smaller species which might have blurred significant size differences which we expected to find.

Oribatid mites are known to be mostly generalist feeders (Schneider & Maraun 2005, Maraun *et al.* 2007) showing selective feeding (‘choosy generalists’) in experiments when high-quality food is available (Schneider & Maraun 2005). Although it is suggested that the strength of co-evolutionary patterns between Oribatida and food sources is rather weak (Salamon *et al.* 2004), we still expected to

see niche partitioning in the group of fungal feeders on which we focused the analysis. From former studies (Schneider *et al.* 2004) it is known that oribatid mites can span over four trophic levels which is an important finding in regard to the application of niche or neutral theory tests: these theories should be applied to the same trophic level as these are the species which are competing for the same resources and analyses will vary in their results otherwise (Maraun *et al.* 2011, Chapter 2). For the first time, we here use stable isotope analysis for a priori grouping of species into feeding groups which are supposed to actually compete for the same resources.

In general, stable isotope analysis is a very powerful tool to assign species to feeding groups. It reflects long-term feeding which can then be interpreted in terms of trophic niche differentiation independent from short-term environmental changes (Maraun *et al*. 2011). However, as we have seen in our analysis, this method has its limitations: In general, it is nearly impossible to distinguish between food items which have been ingested actively or by accidently by oribatid mites (unless egestion is also extensively studied (Scheu 2002)) which is not only a problem in stable isotope but also gut content analysis. Additionally, for assigning species to feeding groups, measurements of potential resources are needed. As Corral-Hernández *et al.* (2015) indicated, the use of litter is not an appropriate food resource for oribatid mite communities as they don't feed on the litter but on microorganisms or lichens, algae, etc. (see Appendix, Fig. B S2). Interestingly, there is evidence that oribatid mites prefer dark pigmented fungi which should be taken into consideration as potential food resource (measurement of spores, e.g.). The more differentiated the selected potential food sources are, the higher the resolution of the analysis will be. However, there will always be species which might not match completely to one or the other group. Dependent on how abundant these species are, they might change the outcome of analyses based on the assignment to a certain feeding group. Still, we want to highlight $^{13}C/^{15}N$ analysis as powerful tool for trophic group assignment of soil microarthropods and in our case the a priori grouping indeed had a positive effect on the results. We also tried to find evidence of niche partitioning by using the stable isotope signatures in correlations, but also here we did not find significant results. Additionally, we tested if closely related species differ strongly in their trophic niches which has been shown for gamasid mites (Klarner *et al*. 2014) and lithobiids (Ferlian *et al.* 2012), however, we did not find evidence for this. At this point, it might be assumed, as Maraun *et al.* (2007) suggested, that the trophic niches we are looking for are already available at a very small scale (<1mm) and thus by far smaller than our sampling design can capture. The authors suggest that the high local abundance and diversity of oribatid mites might be attributed to their ability of selecting very small food particles like fungi, bacteria and others. However, there is theoretical and experimental evidence that food resources are actually limited in soil (Slobodkin *et al.* 1967; Scheu & Schaefer 1998) which is why we are still convinced that it is an important driver for competition. Further investigation with other methods, e.g. gut content or phospholipid fatty acid analysis, but also the spatial and temporal distribution of food resources should be conducted to resolve this issue. In this context, the term 'trophic plasticity' comes into play: there are only few

studies dealing with this topic (e.g. Gan *et al.* 2014, Corral-Hernández *et al.* 2015). There is evidence that species occupy similar niches across studies (Erdmann *et al.* 2007; Fischer *et al.* 2010; Maraun *et al.* 2011; Perdomo *et al.* 2012), however, contrasting results are also available (Corral-Hernández *et al.* 2015) where some species show significant differences in their stable isotope signatures across six different oak forests. The topic of plasticity should receive more attention in this context as it might be an important clue to ressolve mechanisms behind coexistence.

Neutral based processes

As our focus is on soil mesofauna, which is between 100µm and 2mm in size, it is necessary to think about an appropriate scale for studying mechanisms of coexistence. One of the most important factors for mobile organism groups like microarthropods is dispersal. In our study, we suppose that our sampling design of 15x15m plot size is appropriate to avoid dispersal limitation given our target organism group (Ojala & Huhta 2001, Lehmitz *et al.* 2012). It is known that mobile organisms show diurnal vertical movements and preferences in terms of abiotic conditions which can be potential mechanisms behind the avoidance of competition, an assumption which is also based in the metacommunity concept. For this reason we cut the soil cores into 2cm slices, collected information about where species are and if this changes with season and included it as a factor in further analyses. In chapter 2, we show that the depth distribution does not play an important role in the structuring of the community and hence does not give evidence for segregation of potentially competing species. By conducting a co-occurrence analysis (see Appendix, Table D 1), we were also able to test for the assumption that closely related species should segregate most as they are supposed to have very similar traits. We found no evidence for this aspect which supports the effect of the environment which selects for similar traits irrespective of species identity. Therefore, we searched for species pairs, irrespective of being closely related, showing segregation pattern. Indeed, the analysis revealed some species pairs which showed at least significant effect size for segregation, however, a closer look at the original data revealed that these species only seldomly occurred in the same sample after all. We hence do not see this as a strong evidence for spatial segregation. However, the approach of co-occurrence analysis is straightforward given the occurrence of species is well replicated. Additionally, most of the respective pairs were not consistent over the seasons. We attribute this on the one hand to the statistical problem described above but also to potential population dynamics which cannot be resolved with our sampling design which is based on two samplings only. The latter assumption is supported by the fact that we found seasonal differences which cannot be attributed to differences in environmental parameters, e.g. (see Appendix, Fig. B S1) which in summary offers interesting starting points for future studies and should be investigated in more detail. Temporal segregation could be an important factor driving the coexistence of species as litter and other materials get broken down by a succession of different fungal species (Hudson 1968, Hayes 1979, Osono 2007) which might result in

a shift of trophic preferences of microarthropod species over time (Maraun *et al.*2011). Additionally, it is not clear if and how the preferred food resources might change depending on the developmental stage of oribatid mites (but see Schneider *et al.* 2004). Also the availability of resources might change with time and also depth. Scheu and Falca (2000) found that the trophic niche actually seems to be independent from the current location in terms of depth distribution which indicates that oribatid mites seem to not change their diet along environmental gradients and hence in different habitats (Maraun *et al.* 2007). This finding is also supported by other studies which suggest that adult oribatid mites do not occupy specific microhabitats (Hansen 2000, Horwood & Butt 2000, Osler & Beattie 2001) in contrast to immature instars (Schön *et al.* 2009).

Interestingly, in our study, we also could not reject the neutral model of beta diversity, although we have seen that the environmental gradient indeed has a strong influence on the species distribution. This is somehow surprising, however, environmental filtering can actually be consistent with neutral theory: The environment selects for similar species, e.g. in terms of size and diet, which results in similar species being present in the same location (functional equivalence, Hubbell 2005). If species are then generalists enough in terms of food, there might simply be no need for niche partitioning in terms of food, which might be the reason of why in our study we have no evidence for resource competition being a major structuring force.

We showed that environmental and spatial factors representing different theoretical approaches act simultaneously on the examined oribatid mite community. However, we have also seen that each theory has limitations as the function of theories is to provide generalizations and especially simplifications for complex problems. In the context of niche partitioning processes it is hence necessary to include additional mechanisms like how individuals influence their own niche via their activities and metabolic products.

Niche construction

As especially microarthropods can be very abundant locally, their interactions with their abiotic environment should receive more attention. In contrast to earthworms which are economically important, well-studied ecosystem engineers (for summary e.g. Six *et al.* 2004), microarthropods have been neglected in this framework to date which is also a matter of handling issues which have hampered the successful experimentation to date. In chapter 3 we made the attempt to summarize the literature about how microarthropods influence the process of soil aggregation formation. We found a strong bias towards earthworms and termites but also microorganisms like bacteria and fungi. The group of mesofauna (typically represented by springtails and mites) has been neglected, still some potential mechanisms have been proposed but not intensely studied yet. In the future, this issue should be considered as missing link between the impacts of macro- und microfauna, contributing to the

proper functioning of soil which is increasingly important in regard to land use and soil management techniques. However, in the framework of ecological theories, we want to emphasize here that the idea of species obviously affecting their environment should be more often included into studies dealing with community structuring forces and overcome the idea of organisms being passive recipients of environmental influence. At early times of the niche framework development, abiotic factors were seen as given conditions but not as variables which might be changed by the species. However ecologists define the niche today, it is based on the idea that there are always two basic components of a niche which have been described by McInerny and Etienne (2012) as being on the one hand 'the niche as a facet of environment' and on the other hand 'the niche as a facet of species', i.e. the interdependence of species and their environment. This is especially important in terms of how to model dynamical processes like species continuously modifying their environment. Also, the questions of which initial environmental conditions were present when the species colonized the habitat and to which extent species can modify their niche in favor of themselves and potentially in expense of other species, hence directly or indirectly altering competition conditions or natural selection pressure (Post & Palkovacs 2009) come up. What we observe at a particular time of our studies is actually already the result of a long term alteration by all soil organisms on multiple scales, depending on the species' traits. One can imagine interesting cases for studies, when niche construction might change the colonization potential of other species, e.g., and therefore altering competition. It is widely assumed that the neutral theory does not at all consider competition, however, it is implicitly included when it comes to the availability of space for species. The space is limited and niches can only be colonized if there is an empty niche. But what happens if the niche is constantly modified by other species? Can all species still colonize this space with an equal probability? Is dispersal ability a trait which is beneficial in this case to quickly explore new locations? While proponents of Niche Construction Theory (NCT) highlight its potential to integrate ecosystem ecology and evolutionary theory (Odling-Smee *et al.* 2013), one could point out among others that actually each activity of each organism would fall under this theory (Odling-Smee *et al*. 2003, Laland & Odling-Smee 2003, Laland *et al.* 2005) which raises the question if this is a useful concept (e.g. Scott-Phillips *et al*. 2013). At the same time, the question arises if every alteration necessarily has an inter- or intraspecific impact. If one acknowledges the NCT as a standalone concept or part of evolutionary theories, we would like to highlight that it has to be kept in mind although this process will add enormous complexity to any model. However, it is tempting to think about this in more details for oribatid mites and microarthropods in general: if species constantly modify their environment and thus create new microhabitats, would this be enough to increase heterogeneity to a point that high local species diversity can be maintained? Still, the effects of one single species (or even one individual), and hence the interplay of different faunal groupsare little understood but can be assumed to reveal interesting insights into the factors shaping communities. We expect the contributions of these factors to differ from our study in case of potential competition between dispersal limited, fungal feeding

oribatid mites with mobile fungal feeding Collembola, e.g., a situation which is likely and most strongly expected to happen in the first 5cm of the soil horizon where most individuals and species were found.

We have discussed the influence of environmental filtering, niche partitioning, space and dispersal, population dynamics and the effect of the species on their environment, however, there is one more factor which becomes increasingly important: disturbance. We will discuss in the following how disturbances can shape communities and can be detected by neutral models.

Effects of disturbance on community structures

In the metacommunity framework (Leibold *et al.* 2004), sets of local communities are embedded in a landscape and at the same time connected by dispersal of the respective species. The landscape might also consist of heterogeneous patches, e.g. in form of environmental gradients. Finally, there are additional factors which might act simultaneously and are included in this framework like species sorting, mass effect and patch dynamics (for details see Introduction). On top of all these factors, disturbance events might have an effect which we discuss in chapter 4. Here, we use neutral models which can function as a null hypothesis of estimations of beta diversity which can then be compared to the observed beta diversity of a community. We used oribatid mite data sets ranging from relatively undisturbed sites like grasslands and beech forest stands to extremely disturbed sites like heavy metal polluted grass stands to Mediterranean maquis plots which experienced a high-intensity fire-treatment during an experiment. There are studies (for review see Behan-Pelletier 1999) suggesting that oribatid mites are sensitive to disturbances of any kind and strength which leads to the assumption that the intermediate disturbance hypothesis might not apply to this group of microarthropods and makes them suitable bioindicators also for long-term disturbances (e.g. Hülsmann & Wolters 1998, Behan-Pelletier 1999, Maraun & Scheu 2000, Arroyo & Iturrondobeitia 2006, Andrés *et al*. 2011, Luptácik *et al*. 2012, Al-Assiuty *et al.* 2014). We here bring forward the use of beta diversity to detect changes in the community due to disturbances (see Anderson *et al.* 2006, 2011; Dornelas *et al.* 2006; Caruso *et al.* 2012a,b). The effects of disturbance depends on the one hand on the type but also on the intensity which then can have non-predictable effects on community structures and of course on the different community members. Another outcome of disturbance is also expected when key resources are removed, which can be trees, e.g., which provide habitat for numerous species in contrast to scenarios where 'only' smaller organisms go extinct (Syms & Jones 2000). This is especially the case if underlying mechanisms are not known. It is assumed that moderate disturbance can promote local diversity (Intermediate Disturbance Hypothesis) as dominant species are reduced and hence competitively inferior species can persist (Connell 1978, Petraitis *et al.* 1989). In contrast, extreme disturbances can severely reduce diversity and eliminate species which results in a restructuring of the community (Petraitis *et al*. 1989). Studying the effects of disturbance has become a necessity and will

become increasingly important. We here provide a method which aims at monitoring changes in beta diversity which can be useful in this context.

There are various ways of how beta diversity can be measured and linked to alpha and gamma diversity (Kraft *et al*. 2011, Legendre & de Caceres 2013, Myers *et al.* 2013); we use the beta diversity definition provided by Legendre & de Caceres (2013) where beta diversity is the total variance of the community matrix. This is advantageous in terms of having summarized beta diversity in one easy to calculate number which is still not calculated from alpha and gamma diversity (Kraft *et al.* 2011) but still dependent from it by using a general neutral model. The observed level of beta diversity was compared to the simulated beta diversity distribution which could result in three different outcomes in terms of the observed beta diversity (BD): (1) BD equals, (2) is larger (divergence), or (3) is smaller (convergence) than the neutral prediction. We tested if and how various levels in terms of type and strength of disturbance might lead to either divergence or convergence. In our analyses, we observed all three outcomes which we explained in detail in chapter 4. Although it needs to be clearly stated that this modeling approach does not aim at identifying potential mechanisms of how the respective disturbance affects community structures, it is possible to detect and then interpret the outcome in terms of possible effects on the basis of knowledge about the respective studying area. Here, the expectations derived from neutral frameworks have again shown to be a valuable tool as a null hypothesis for monitoring purposes also on larger scales, depending on the expected source of disturbance. In terms of intense land use practices, global change and increasing species loss, it is important to understand also the dynamics of other soil animal groups (Clark 2009, Blankinship *et al.* 2011, Eisenhauer *et al.* 2012). We here propose the neutral model approach we presented as a useful, easy to apply tool for monitoring purposes which will give us insight of the potential consequences for biodiversity and hence ecosystem function on larger scales.

Conclusion

Im summary, we show that the application of different techniques improve the overall insight into the opaque habitat of soil. What we should have understood from the last centuries' ecological research is that for each example of a theory or rule it is possible to find more or less easily at least one exception in nature. This might not only be due to different habitats but also simply by looking at the same target organism in the same habitat but on different scales (McInerny & Etienne 2012). The studies presented here underline the necessity of simple models and theoretical frameworks which can then be extended stepwise with additional assumptions to increase realism. As especially soil is very complex, there is a need for reducing this complexity to a couple of testable assumptions which finally has to result in different definitions of the niche depending not only on the habitat type but also on the target organisms and the ecologists' rating of important factors he or she wants to focus on.However, we also

want to highlight the necessity of providing clear definitions about the respective views of the niche in all studies to make comparisons among studies easier and provide a clear basis for discussions.

Not only in ecology, but also in all fields of science, there is always a trade-off for theories: We have to reduce complexity to be able to understand underlying mechanisms at the expense of realism (Pickett *et al.* 2007). And although some theories' assumptions might be completely unacceptable or illogical at first glance, they might provide a useful alternative to existing theories and might be used as a null model, e.g. The procedure of combining assumptions of different theoretical frameworks has brought up interesting studies (Purves & Pacala 2005, Chisholm & Pacala 2010, Haegeman & Etienne 2011, Haegeman & Loreau 2011) where niche structures are added to neutral models or the intensities of interspecific vs intraspecific competitionare varied. The results were sometimes surprising, but all studies provided evidence that neutral and niche based assumptions are complementing and hence valuable for the description of species' niches.

Finally, we conclude that (1) environmental filtering and niche partitioning are distinct but interacting processes which should be taken into account in future studies, (2) we were not able to find 'the niche' of our species by using core ecological concepts like the limiting similarity concept, (3) temporal segregation should be investigated in more detail (including resource availability), (4)the influence of organisms on their local habitat needs to be studied in detail as another important factor shaping communities, (5) neutral models are useful as null model for testing for niche based assumptions. We see our studies as starting points for future research combining different methodologiesand scale to gain detailed insight into not only soil microarthropod communities.

6 Summary

The overall aim of this dissertation was to evaluate the relative roles of niche and neutral based processes like environmental filtering, niche partitioning, dispersal and biotic interactions as forces structuring soil oribatid mite communities on different scales. We used different methods and theoretical approaches to gain an extensive insight into an oribatid mite community in a dry grassland in Germany but also into published data sets of oribatid mite communities from different habitats.

In chapter 2, we conducted a field study based on a small-scale spatially explicit sampling design along an environmental gradient of a hillside in a dry grassland in Brandenburg, Germany. In spring and autumn 2012, we took soil cores (10cm long, Ø 5cm) and cut them into five 2cm slices to account for depth distribution of the species. We measured %water, pH, content of C and N as well as soil structure to account for major environmental variables of the location. We determined the oribatid mite community to species level, measured the body length of each individual and analyzed the stable isotope ratios $^{12}C/^{13}C$ and $^{14}N/^{15}N$ to assign species to feeding groups (i.e. fungal feeders/secondary decomposers, predators/scavengers, moss feeders, lichen feeders, etc.). For the first time, we apply niche and neutral based theories to one trophic level only which is an important but mostly ignored prerequisite. We found evidence for environmental filtering with organic matter content (i.e. content of C and N) and soil structure being the major predictors for community variance. When we tested for potential mechanisms behind niche partitioning in terms of the limiting similarity concept we did not find evidence for segregation via body size, trophic niche or depth distribution. However, our data support the hypothesis that temporal segregation based on population dynamics might play an important role and should be investigated in more detail in future studies.

In chapter 3, we compiled the available literature about the effects of soil microarthropods on soil aggregation. We found a gap in the literature which might be due to handling issues during experimentation. Still, we were able to discuss potential mechanisms which can be divided into direct and indirect mechanisms. Direct mechanisms include the provision of organic material in form of faecal pellets, molts, etc. which can act as starting points for microaggregates. High local abundance of microarthropods might cause damage via feeding to the hyphal enmeshment of soil aggregates which might decrease soil aggregate stability. Organic material can additionally serve as nutrient source for microorganisms, hence increasing their growth amd increasing soil aggregation formation. Additionally, the selective feeding and transport of microbes on the cuticle of microarthropods indirectly affect soil aggregation. Finally, the interactions between soil microarthropods and bigger or smaller soil fauna need to be studied further as we expect various positive effects on soil aggregation in this context. Overall, we suggest to study the effects of microarthropods on soil aggregation in more details as this would broaden our knowledge on the one hand in terms of how beneficial this soil

faunal group can be for soil restoration, e.g., but also to understand how organisms affect their local environment.

In chapter 4, we performed a data synthesis based on a literature research to find oribatid mite data sets which we used together with our own data to show the usefulness of neutral models to detect changes in beta diversity. Changes in beta diversity can act as biotic indicator of disturbance and we propose a straightforward method to be used in practice. Therefore, the beta diversity of the observed data set is calculated and then compared to its neutral counterpart. There are three different possible outcomes: the observed data set can be larger (divergence), equal to or smaller (convergence) than the neutral prediction. If disturbance is taking place, we expect to see either divergence or convergence, depending on type and strength of the disturbance. We discuss how this procedure can be used as monitoring tool.

In summary, we have investigated which forces have effects on community structures and how their relative roles can change with scale. We have also seen that the impact of the organisms on their own local environment might have severe implications on the outcome of competition, e.g., which should be studied in more detail. Finally, we present an approach based on neutral model for long term monitoring purposes which is based on changes in beta diversity of the respective communities. In this work, we show that our approach which was based on different theories and methodologies, reveals very interesting findings about soil oribatid mite communities in dry grasslands but also other habitats.

7 Zusammenfassung

Das übergeordnete Ziel dieser Dissertation war es, die relativen Einflüsse von Prozessen, die die Struktur von Bodenarthropodengemeinschaften beeinflussen, zu untersuchen. Diese Prozesse, wie das Filtern von Arten durch Umwelteinflüsse und Nischenpartitionierung, aber auch Ausbreitungslimitierung und biotische Interaktionen, agieren auf unterschiedlichen Größenordnungen. Wir bedienten uns unterschiedlicher Techniken und theoretischer Ansätze, um einen möglichst umfassenden Einblick in eine Hornmilbengemeinschaft in einem Trockenrasen in Deutschland aber auch aus bereits publizierten Daten von anderen Habitaten zu bekommen.

In Kapitel 2 führten wir eine Feldstudie durch, die auf einem kleinskaligen, räumlich expliziten Studiendesign basiert. Dazu beprobten wir im Frühjar und Herbst 2012 einen Umweltgradienten entlang eines Hügels in einem Trockenrasen in Brandenburg (Deutschland). Wir nahmen Bodenkerne (10cm lang und Ø 5cm), die wir in fünf 2cm breite Streifen schnitten, um die vertikale Verteilung der Arten in unseren Analysen berücksichtigen zu können. Zudem bestimmten wir den Wassergehalt, pH-Wert, Gehalt an Kohlenstoff und Stickstoff sowie die Bodenstruktur als Hauptumweltfaktoren. Wir bestimmten die Oribatidengemeinschaft auf Artniveau, maßen alle Körperlängen der adulten Oribatiden und analysierten die Isotopensignaturen der jeweiligen Arten ($^{12}C/^{13}C$ und $^{14}N/^{15}N$). Basierend darauf konnten wir die jeweiligen Arten in funktionelle Gruppen einteilen (Pilzfresser, Räuber, Moos- bzw. Flechtenfresser, Zersetzer und endophage Arten). Zum ersten Mal nutzen wir diese Information, um nischen- und neutrale Theorien auf nur eine Trophieebene anzuwenden, wie es ursprünglich vorgesehen aber meist nicht umgesetzt ist. Der Gehalt an organischem Material (Gehalt an Kohlenstoff und Stickstoff) und die Bodenstruktur zeigen einen großen Einfluss auf die Oribatidengemeinschaft, was ein Hinweis darauf ist, dass Umweltfaktoren einen Filter für potentielle Besiedlerarten darstellen. Im nächsten Schritt beleuchteten wir mögliche Mechanismen hinter Nischenpartitionierung wie sie durch das *limiting similarity concept* beschrieben werden, z.B.Einnischung über Unterschiede in Körpergrößen, Trophieebene oder dievertikale Verteilung entlang des Bodenprofils, fanden aber keinerlei Zusammenhänge. Unsere Daten weisen aber auf saisonale Unterschiede, die nur durch Populationsdynamiken erklärbar sind, was in zukünftigen Studien berücksichtigt werden sollte.

In Kapitel 3 erstellten wir eine Übersicht über die verfügbare Literatur zum Thema „Effekte von Mikroarthropoden auf Bodenaggregation“. Es zeigte sich, dass zu diesem Thema sehr wenig Studien vorliegen, was unter anderem darin begründet sein kann, dass die Handhabung von Mikroarthropoden in Experimenten und Feldstudien nicht einfach ist. Trotzdem konnten wir direkte und indirekte Mechanismen in diesem Zusammenhang diskutieren. Direkte Mechanismen bestehen einerseits in der Bereitstellung von organischem Material in Form von Kotballen, Häutungsprodukten usw., die als Startpunkt für Mikroaggregate dienen können. Andererseits kann eine hohe lokale Abundanz von

Mikroarthropoden negative Auswirkungen auf aggregatstabilisierende Hyphennetzwerke haben, indem an diesen gefressen wird. Gleichzeitig kann das organische Material sich aber auch indirekt positiv auf die Stabilität und Bildung von Aggregaten auswirken, in dem es als Nährstoffquelle für Mikroorganismen dient und somit deren Wachstum erhöht. Zusätzlich beeinflussen selektives Abweiden von Mikrobenmatten und deren passiver Transport an der Kutikula von Mikroarthropoden indirekt die Bildung von Aggregaten. Ein weiterer komplexer, noch wenig untersuchter aber wichtiger Mechanismus liegt in der Interaktion der unterschiedlich großen Bodenfauna, die wahrscheinlich größtenteils positiver Natur sein wird. Wir kommen zu dem Schluss, dass den Effekten von Mikroarthropoden auf Bodenaggregation in Zukunft mehr Aufmerksamkeit geschenkt werden sollte, da das Verständnis der zugrundeliegenden Mechanismen nicht nur für die Landwirtschaft, sondern auch in Hinsicht auf Effekte von Organismen auf ihre Umwelt im Kontext von Nischentheorien nutzbringend ist.

In Kapitel 4 führten wir auch eine Literaturrecherche durch, um Daten über Hornmilbengemeinschaften von unterschiedlichen Habitaten zu finden und diese und unsere eigenen Daten unter einem neuen Gesichtspunkt zu analysieren. Wir nutzten neutrale Modelle, um Änderungen in der beta-Diversität festzustellen, die in der Praxis als Indikator für Störungen bewertet werden können. Dafür wird als erstes die beta-Diversität des orginalen Datensatzes berechnet. Auf der Grundlage dieser Originaldaten werden 4999 simulierte neutrale Pendants berechnet und deren beta-Diversitätverteilung mit dem beta-Diversitätswert des Originaldatensatzes verglichen. Dabei sind drei unterschiedliche Ergebnisse möglich: der Wert des Originaldatensatzes ist größer (Divergenz), gleich groß oder kleiner (Konvergenz) als der der neutralen Simulationen. Wenn tatsächlich eine Störung im System vorliegt, wird dies durch Divergenz oder Konvergenz deutlich, abhängig von Stärke und Art der Störung. Abschließend diskutieren wir, wie diese Vorgehensweise als einfach zu handhabendes Hilfsmittel in der Praxis eingesetzt werden kann.

In dieser Arbeit konnte gezeigt werden, dass sich der Einfluss der zugrunde liegenden Mechanismen je nach betrachteter Größenordnung ändert. Zusätzlich wurde herausgearbeitet, dass Bodenorganismen einen noch recht unbekannten Einfluss auf ihre direkte Umwelt haben können und dieser unter Umständen auch Auswirkungen auf den Ausgang von Konkurrenzsituationen haben kann. Abschließend präsentieren wir eine praktische Vorgehensweise, um Störungen in Habitaten anhand von beta-Diversität und neutralen Modellen zu identifizieren. Mit Hilfe verschiedener theoretischer und methodischer Ansätze erhielten wir einen Überblick über die Kräfte, die auf die Strukturierung von Oribatidengemeinschaften im Boden verschiedender Habitate wirken.

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9 Contribution to chapters

chapter 2: Maaß, S., Maraun, M., Scheu, S. Rillig, M.C., Caruso, T. 2015. Environmental filtering vs. resource-based niche partitioning in diverse soil animal assemblages. Soil Biology and Biochemistry 85: 145-152.

own contribution: I did the field sampling with the help of Tancredi Caruso, conducted the lab work, namely extraction, sorting, identification and size measurements of arthropods and the measurement of environmental variables of the soil (pH, water content, C and N content, dry and wet sieving). With the help of Mark Maraun and Susanne Böning-Klein (Tech. Assist.) I conducted the preparation of the samples for stable isotope analysis in the University of Göttingen (AG Tierökologie, Prof. S. Scheu). I did the statistical analysis with the help of Tancredi Caruso and wrote the manuscript.

chapter 3: Maaß, S., Caruso, T., Rillig, M.C. 2015. Functional role of microarthropods in soil aggregation. Pedobiologia 58: 59-63.

own contribution: I conducted the literature researchand wrote the manuscript.

chapter 4: Maaß, S., Migliorini, M, Rillig, M.C., Caruso, T. 2014. Disturbance, neutral theory and patterns of beta diversity in soil communities. Ecology and Evolution 4: 4766-4774.

own contribution: I conducted the literature research as well as the statistical analyses with the help of Tancredi Caruso and Massimo Migliorini and wrote the manuscript.

10 Appendix

Appendix A. Information about soil oribatid mite community

Table A S 1 List of family and species names, species code, abundance in the respective seasons, mean body length ± SE, depth score based on weighted average in cm, and stable isotope measurements with resulting feeding group assignment (f = fungal feeder/secondary decomposer, l =lichen feeder, e = species with endophagous juveniles, p = predator, mo = feeding on mosses, my = mycophagous, d = decomposer, ? = not known).

family	species	species code	abundance (n of ind.)		mean body length (µm) ± S.E.	depth score (weighted average) in cm	stable isotope signatures			
			May 2012	Oct 2012			mean ^{13}C ± STDEV	mean ^{15}N ± STDEV	n of measurements	assigned feeding group
Achipteriidae	*Achipteria coleoptrata*	s32	1	0	565	4	-26.16 ± 0.00	-1.01 ± 0.00	1	f
Carabodidae	*Carabodes willmanni*	s28	0	3	447 ± 22.37	1	-25.35 ± 0.00	-6.83 ± 0.00	1	l
Ceratozetidae	*Trichoribates incisellus*	s22	12	15	437 ± 4.41	2.4	-18.72 ± 9.28	4.22 ± 7.42	2	f
	Trichoribates novus	s33	1	0	710	5	-26.68 ± 0.00	3.20 ± 0.00	1	?
Chamobatidae	*Chamobates birulai*	s26	2	2	453 ± 11.62	2.7	-25.69 ± 0.00	1.54 ± 0.00	1	f
Damaeidae	*Porobelba spinosa*	s29	48	27	394 ± 5.26	1.1	-25.24 ± 0.02	3.21 ± 0.20	2	p
Epilohmanniidae	*Epilohmannia cylindrica*	s16	8	4	513 ± 5.59	6.8	-24.40 ± 0.14	-2.56 ± 0.93	2	e
Euphthiracaridae	*Rhysotritia ardua*	s10	6	6	636 ± 9.20	3.6	-24.67 ± 0.21	-3.19 ± 0.39	1	e
Galumnidae	*Galumna obvia*	s13	0	4	659 ± 6.22	1	-26.06 ± 0.33	-1.56 ± 0.61	3	f
	Pergalumna nervosa	s15	12	83	670 ± 2.41	1.9	-25.28 ± 0.18	-0.36 ± 0.42	3	f
Haplozetidae	*Protoribates capucinus*	s18	9	14	355 ± 2.29	5.5	-25.95 ± 0.18	-2.22 ± 0.11	2	f
Liacaridae	*Liacarus coracinus*	s25	18	9	731 ± 22.87	1.4	-25.88 ± 0.17	-1.82 ± 0.47	3	f
Mycobatidae	*Punctoribates punctum*	s2	195	147	360 ± 0.98	1.5	-25.25 ± 0.15	-0.05 ± 0.08	3	f
	Minunthozetes semirufus	s31	0	3	299 ± 1.21	5	-26.91 ± 0.00	-1.04 ± 0.00	1	m
Oppiidae	*Oppiella nova*	s8	33	54	268 ± 2.24	1.4	-25.21 ± 0.02	1.18 ± 1.01	2	f
	Microppia minus	s19	69	79	174 ± 2.29	2.5	-25.09 ± 0.00	3.76 ± 0.00	1	p
	Dissorhina ornata	s30	134	10	274 ± 2.10	1	-25.85 ± 0.05	0.85 ± 0.30	2	f
Passalozetidae	*Passalozetes perforatus*	s7	2	2	325 ± 1.01	1.3	-23.99 ± 0.00	1.56 ± 0.00	1	my
Phenopelopidae	*Peloptulus phaenotus*	s4	162	105	437 ± 1.79	1.7	-25.93 ± 0.13	-1.81 ± 0.20	3	f
	Eupelops occultus	s23	22	11	471 ± 3.92	1.4	-26.11 ± 0.07	0.46 ± 0.54	3	f

	Eupelops tardus	s11	28	32	472 ± 3.12	1.5	-25.95 ± 0.09	0.02 ± 0.16	3	f
Scheloribatidae	*Liebstadia pannonica*	s5	254	400	361 ± 0.80	1.2	-25.06 ± 0.21	0.70 ± 0.47	3	f
	Scheloribates laevigatus	s12	40	54	550 ± 2.13	1.5	-25.48 ± 0.05	-2.09 ± 0.05	3	f
	Scheloribates quintus	s14	22	57	428 ± 2.52	1.3	-25.28 ± 0.20	0.72 ± 0.04	3	f
Scutoverticidae	*Scutovertex sculptus*	s3	3	3	558 ± 4.31	1.3	-27.38 ± 0.19	-3.93 ± 0.15	2	d
Suctobelbidae	*Suctobelbella sarekensis*	s24	20	15	210 ± 4.80	1.3	-25.76 ± 0.00	1.00 ± 0.00	1	f
Tectocepheidae	*Tectocepheus velatus alatus*	s1	1	1	296 ± 4.54	1	-26.16 ± 0.00	0.43 ± 0.00	1	f
	Tectocepheus velatus sarekensis	s6	104	45	303 ± 1.05	1.4	-26.81 ± 0.03	-2.80 ± 0.01	3	d

Appendix B. Supplementary information for Chapter 2

Seasonal variation in environmental gradients

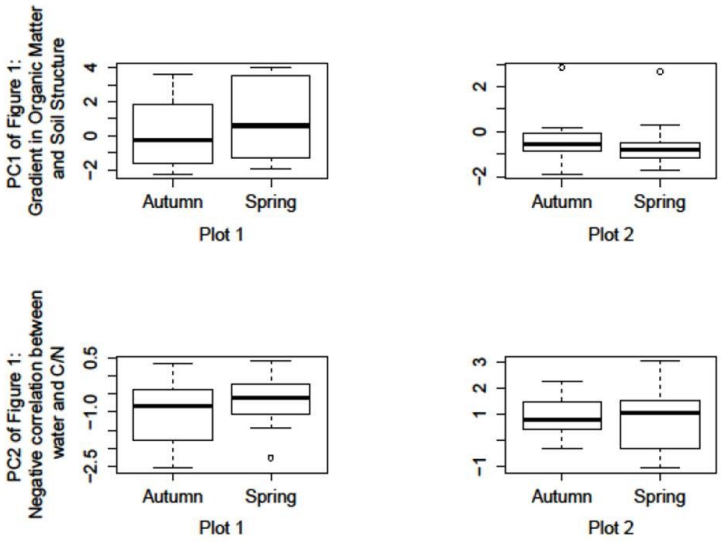

Figure B S 1 The four Box-and-whisker plots of the first two PCA axes of Fig. 1(environmental gradients) show seasonal differences across the two sampling plots. There is no significant difference between spring and autumn for both plots.

Stable isotope signatures

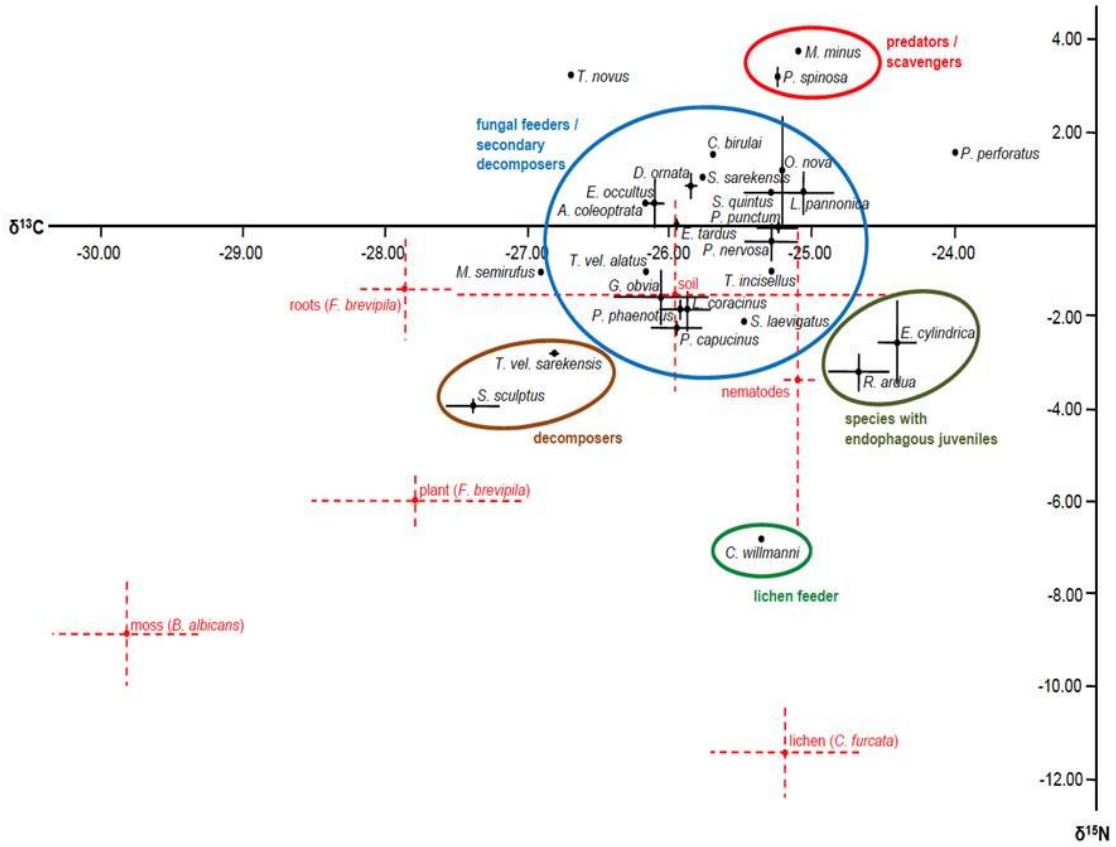

Figure B S 2 Mean (± standard deviation) of ^{13}C and ^{15}N signatures of the 28 species for which isotopic information could be obtained(for full names and other information see also Table B S2 and S3). Groups (coloured circles) were defined based on literature on isotopes in soil animals, which we used to complement our own original data. The blue circle groups fungal feeders/secondary decomposers; the yellow circle groups the decomposers; the green circle groups species with endophagous juveniles; the red circle groups potential nematode predators/ scavengers; circles are drawn by eye and based on literature. Plant and root material are marked with a triangle and provided a baseline for comparison with other publications.

Testing Neutral Models

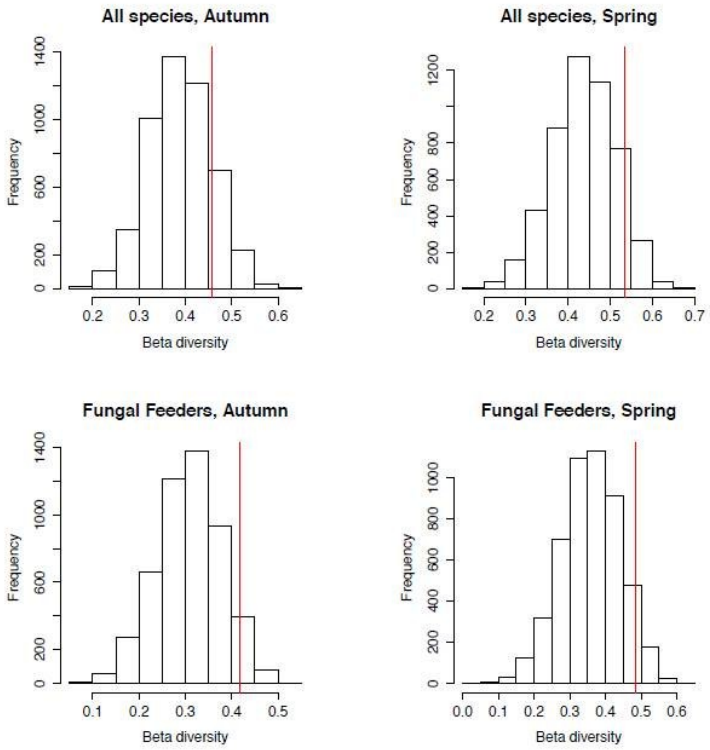

Figure B S 3 Test of neutral model predictions of beta diversity. Histograms show the null distribution of simulated beta diversity values, which we built from the estimates of neutral model parameters (Table B S4). The red line is observed beta diversity. In all case observed beta diversity is higher than the central tendency of the null distribution. However, in all cases none of the assemblages differed significantly from the neutral prediction (all species autum: $p = 0.16$, all species spring: $p = 0.10$, fungal feeders autumn: $p = 0.10$, fungal feeders spring: 0.07). Effect size was more pronounced in the fungal feeder data sets (bottom histograms).

Table B S 1 Summary statistics of environmental variables in the two plots.Mean (± standard error), and minimum and maximum value of Water (% s.d.w.), pH, total N (% s.d.w.), organic C (% s.d.w.) and mean weight diameter (MWD, an index of soil structure) are reported.

	water%		**pH**		**N%**		**C%**		**MWD**	
	mean ± SE	min max	mean ± SE	min max	mean ± SE	min max	mean ± SE	min max	mean ± SE	min max
macroplot 1	8.80 ± 1.39	5.51 12.53	7.30 ± 1.16	5.73 8.94	0.08 ± 0.01	0.01 0.21	1.17 ± 0.18	0.15 2.96	0.43 ± 0.07	0.15 1.15
macroplot 2	9.67 ± 1.53	5.31 15.38	5.27 ± 0.83	4.75 6.87	0.07 ± 0.01	0.03 0.26	0.93 ± 0.15	0.41 3.49	0.29 ± 0.05	0.16 0.53

Table B S 2 Species list including: family name, abundances in spring and autumn, weighted mean depth distribution, and body length.Mean depth distribution was calculated on the basis of relative abundances along six depth levels (slice 1: 1-2cm; slice 2: 3-4cm; slice 3: 5-6cm; slice 4: 7-8cm; slice 7: 9-10cm).

family	species	mean body length (µm) ± S.E.	abundance (n of ind)		mean depth distribution (cm)
			May 12	Oct 12	
Achipteriidae	*Achipteria coleoptrata*	565	1	0	4.0
Carabodidae	*Carabodes willmanni*	447 ± 22.37	0	3	1.0
Ceratozetidae	*Trichoribates incisellus*	437 ± 4.41	12	15	2.4
	Trichoribates novus	710	1	0	5.0
Chamobatidae	*Chamobates birulai*	453 ± 11.62	2	2	2.7
Damaeidae	*Porobelba spinosa*	394 ± 5.26	48	27	1.1
Epilohmanniidae	*Epilohmannia cylindrica*	513 ± 5.59	8	4	6.8
Euphthiracaridae	*Rhysotritia ardua*	636 ± 9.20	6	6	3.6
Galumnidae	*Galumna obvia*	659 ± 6.22	0	4	1.0
	Pergalumna nervosa	670 ± 2.41	12	83	1.9
Haplozetidae	*Protoribates capucinus*	355 ± 2.29	9	14	5.5
Liacaridae	*Liacarus coracinus*	731 ± 22.87	18	9	1.4
Mycobatidae	*Punctoribates punctum*	360 ± 0.98	195	147	1.5
	Minunthozetes semirufus	299 ± 1.21	0	3	5.0
Oppiidae	*Oppiella nova*	268 ± 2.24	33	54	1.4
	Microppia minus	174 ± 2.29	69	79	2.5
	Dissorhina ornata	274 ± 2.10	134	10	1.0
Passalozetidae	*Passalozetes perforatus*	325 ± 1.01	2	2	1.3
Phenopelopidae	*Peloptulus phaenotus*	437 ± 1.79	162	105	1.7
	Eupelops tardus	472 ± 3.12	28	32	1.5
	Eupelops occultus	471 ± 3.92	22	11	1.4
Scheloribatidae	*Liebstadia pannonica*	361 ± 0.80	254	400	1.2
	Scheloribates laevigatus	550 ± 2.13	40	54	1.5
	Scheloribates quintus	428 ± 2.52	22	57	1.3
Scutoverticidae	*Scutovertex sculptus*	558 ± 4.31	3	3	1.3
Suctobelbidae	*Suctobelbella sarekensis*	210 ± 4.80	20	15	1.3
Tectocepheidae	*Tectocepheus velatus alatus*	296 ± 4.54	1	1	1.0
	Tectocepheus velatus sarekensis	303 ± 1.05	104	45	1.4

Table B S 3 Mean (± standard deviation) of delta 13C and 15N of 28 out of the 33 species found in the grassland.Assignation to a trophic group is based on our own results and the literature: f = fungal feeder/secondary decomposer, l = lichen feeder, e = species with endophagous juveniles, p = predator, mo = feeding on mosses, my = mycophagous, d = decomposer, ? = not known.

	mean ^{13}C	mean ^{15}N	n of measurements	trophic group
A. coleoptrata	-26.16 ± 0.00	-1.01 ± 0.00	1	f
C. birulai	-25.69 ± 0.00	1.54 ± 0.00	1	f
C. willmanni	-25.35 ± 0.00	-6.83 ± 0.00	1	l
D. ornata	-25.85 ± 0.05	0.85 ± 0.30	2	f
E. cylindrica	-24.40 ± 0.14	-2.56 ± 0.93	2	e
E. occultus	-26.11 ± 0.07	0.46 ± 0.54	3	f
E. tardus	-25.95 ± 0.09	0.02 ± 0.16	3	f
G. obvia	-26.06 ± 0.33	-1.56 ± 0.61	3	f
L. coracinus	-25.88 ± 0.17	-1.82 ± 0.47	3	f
L. pannonica	-25.06 ± 0.21	0.70 ± 0.47	3	f
M. minus	-25.09 ± 0.00	3.76 ± 0.00	1	p
M. semirufus	-26.91 ± 0.00	-1.04 ± 0.00	1	m
O. nova	-25.21 ± 0.02	1.18 ± 1.01	2	f
P. capucinus	-25.95 ± 0.18	-2.22 ± 0.11	2	f
P. nervosa	-25.28 ± 0.18	-0.36 ± 0.42	3	f
P. perforatus	-23.99 ± 0.00	1.56 ± 0.00	1	my
P. phaenotus	-25.93 ± 0.13	-1.81 ± 0.20	3	f
P. punctum	-25.25 ± 0.15	-0.05 ± 0.08	3	f
P. spinosa	-25.24 ± 0.02	3.21 ± 0.20	2	p
R. ardua	-24.67 ± 0.21	-3.19 ± 0.39	1	e
S. laevigatus	-25.48 ± 0.05	-2.09 ± 0.05	3	f
S. quintus	-25.28 ± 0.20	0.72 ± 0.04	3	f
S. sarekensis	-25.76 ± 0.00	1.00 ± 0.00	1	f
S. sculptus	-27.38 ± 0.19	-3.93 ± 0.15	2	d
T. incisellus	-18.72 ± 9.28	4.22 ± 7.42	2	f
T. novus	-26.68 ± 0.00	3.20 ± 0.00	1	?
T. vel. alatus	-26.16 ± 0.00	0.43 ± 0.00	1	f
T. vel. sarekensis	-26.81 ± 0.03	-2.80 ± 0.01	3	d

Table B S 4 Estimates of neutral model parameters (theta and I) for four data sets: all species spring, all species autumn, fungal feeders spring, fungal feeders autumn.None of the assemblages could reject a general neutral model of beta diversity as shown by the P-values, which are calculated from the method explained in Maass*et al* (2015). See also Figure 3 in the main text. The data set comprising fungal feeders only, however, showed a trend towards divergence, that is that observed assemblages had beta diversity higher then predicted.

	theta	**I**	**p-value**
all species spring	5.79	5.7	0.10
all species autumn	6.02	9.0	0.16
fungal feeders spring	3.68	5.0	0.07
fungal feeders autumn	3.71	7.5	0.10

Appendix C. Supplementary information for Chapter 4

Fitting Neutral Model

We used the method and Pari/Gp functions provided by Etiene (2007) to estimate the two parameters (neutral diversity θ and immigration m) of the general neutral model (Hubbell 2011) applied to the species abundance distribution observed in the field. Etienne (2007) provided a sampling formula for multiple samples and the data we provide for each study area are the species by sample matrices to which this formula applies. The example given here is based on the data set of the Heathland (Figure 2, S1d) and the species by sample matrix of this data set is given in the supplementary file 'observed.txt' (Data S4). In this matrix, rows are samples/sites and columns are species. In order to estimate θ and m with the Pari/Gp functions of Etienne (2007), such a matrix needs to be converted into a string following the example given in Etienne (2007). However, once the parameters were estimated, we simulated neutral communities using the function urn2.gp (Etienne 2007) with the following two lines of code:

read("urn2.gp")

for(n=1,4999,urn2(1.92,[1.72,2.00,9.11,1.01,2.56,2.14,1.69,2.46,5.12,1.23],[154,118,86,110,41,108,106,42,19,27],1))

The output of this is given in the supplementary file simData.txt. Note that a new run of these lines will give a different output because of the newly simulated assemblages. However, the average behaviour of properties such as beta diversity is not affected if the number of simulated communities is reasonably high. The urn2.gp string given above is run via a loop that simulates communities 4999 (in practice the function is applied 4999 times). The function takes three parameters: the estimate of θ (in this case 1.92), the estimate of m for each sample/site (in this case the vector [1.72,2.00,9.11,1.01,2.56,2.14,1.69,2.46,5.12,1.23], and the total number of individuals per sample (in this case the vector [154,118,86,110,41,108,106,42,19,27]). Note that actually the immigration parameter is not given as in Hubbell (2001), that is to say in terms of immigration rate, but instead it is given in terms of number of immigrants, called I by Etienne (2007). The relationship between m and I is

$$m = \frac{I}{I + J - 1}$$

To summarise, at the end of the neutral model fitting exercise, two files are necessary to complete the analysis proposed in this paper with the R script provided in Supporting Information 2: observed.txt

(the species by sample matrix obtained from the field; Data S4) and simData.txt (the simulated communities based on the estimate of neutral parameters; Data S5).

urns2.gp-string

```
read("urn2.gp")

ffor(n=1,4999,urn2(1.92,[1.72,2.00,9.11,1.01,2.56,2.14,1.69,2.46,5.12,1.23],[154,118,86,110,41,108,106,42,19,27],1))
```

R code

####Functions used in Maaß et al. 2014. Disturbance, neutral theory and patterns of beta diversity in soil communities.

#The script consists of two parts: in part 1, the functions are defined. In part 2, the the functions are run#

###############PART 1 ##################

####the following function takes three arguments: the data file (data), the number of sites in the data (sites) and the number of time the data were simulated (n)##

####the function converts the output file or the funtcion urn2.gp (Pari/Gp, see Etienne 2007. Ecology Letters, 10, 608–618) in a list of matrices.

####The Beta diversity (BD) of each matrix can then be calculated using the function "beta.div" given in Legendre and De Caceres (2013) Ecology Letters 16, 951-963.

####The function Beta.div is here also included for convenience.

```
listmatrix<-function (data,sites,n)
 {matrix_list<-vector('list',n)
  number<-1:n
  for(k in number) matrix_list[[k]]<-data[((k*sites)-(sites-1)):(k*sites),]
  for(k in number) matrix_list[[k]]<-as.data.frame(t(as.matrix(matrix_list[[k]])))
  for(k in number) colnames(matrix_list[[k]]) [1]<-"a1"
  for(k in number) matrix_list[[k]]<-subset(matrix_list[[k]],a1>-1)
  for(k in number) matrix_list[[k]]<-as.data.frame(t(as.matrix(matrix_list[[k]])))
  matrix_list  }
```

The beta.div function follows. This is here reported as given in Legendre and De Caceres (2013) Ecology Letters 16, 951-963:

```
beta.div <- function(Y, method="hellinger", sqrt.D=FALSE, samp=TRUE, nperm=999, save.D=FALSE, clock=FALSE)
 # Compute estimates of total beta diversity as the total variance in Y,
 # for 20 dissimilarity coefficients or analysis of raw data (not recommended).
 # LCBD indices are tested by permutation within columns of Y.
 # This version includes direct calculation of the Jaccard, Sorensen and Ochiai
 # coefficients for presence-absence data.
  # Arguments --
  # Y : community composition data matrix.
 # method : name of one of the 20 dissimilarity coefficients, or "none" for
#         direct calculation on Y (also the case with method="euclidean").
# sqrt.D : If sqrt.D=TRUE, the distances in matrix D are square-rooted before
#         computation of SStotal, BDtotal and LCBD.
# samp : If samp=TRUE, the abundance-based distances (ab.jaccard, ab.sorensen,
#        ab.ochiai, ab.simpson) are computed for sample data. If samp=FALSE,
#        they are computed for true population data.
# nperm : Number of permutations for test of LCBD.
# save.D : If save.D=TRUE, the distance matrix will appear in the output list.
# clock : If clock=TRUE, the computation time is printed in the R console.
```

```
# License: GPL-2
# Author:: Pierre Legendre, December 2012, April-May 2013
{
 ### Internal functions
 centre <- function(D,n)
  # Centre a square matrix D by matrix algebra
  # mat.cen = (I - 11'/n) D (I - 11'/n)
 {        One <- matrix(1,n,n)
  mat <- diag(n) - One/n
mat.cen <- mat %*% D %*% mat
 }
###
 BD.group1 <- function(Y, method, save.D, per)
 {
  if(method=="profiles") Y = decostand(Y, "total")
  if(method=="hellinger") Y = decostand(Y, "hellinger")
  if(method=="chord") Y = decostand(Y, "norm")
  if(method=="chisquare") Y = decostand(Y, "chi.square")
  #
  s <- scale(Y, center=TRUE, scale=FALSE)^2   # eq. 1
  SStotal <- sum(s)          # eq. 2
 BDtotal <- SStotal/(n-1)   # eq. 3
 if(!per) { SCBD<-apply(s,2,sum)/SStotal }else{ SCBD<-NA }  # eqs. 4a and 4b
 LCBD <- apply(s, 1, sum)/SStotal  # eqs. 5a and 5b
 #
 D <- NA
 if(!per & save.D)   D <- dist(Y)
 #
 out <- list(SStotal_BDtotal=c(SStotal,BDtotal), SCBD=SCBD, LCBD=LCBD,
            method=method, D=D)
}
###
BD.group2 <- function(Y, method, sqrt.D)
{
 if(method == "divergence") {
  D = D11(Y)
      } else if(any(method ==
             c("jaccard","sorensen","ochiai")))
 {
  if(method=="jaccard") D = dist.binary(Y, method=1) # ade4 takes sqrt(D)
  if(method=="sorensen")  D = dist.binary(Y, method=5) #ade4 takes sqrt(D)
  if(method=="ochiai") D = dist.binary(Y, method=7) # ade4 takes sqrt(D)
```

```
  } else if(any(method ==
c("manhattan","canberra","whittaker","percentagedifference","wishart")))
  {
   if(method=="manhattan") D = vegdist(Y, "manhattan")
   if(method=="canberra")  D = vegdist(Y, "canberra")
   if(method=="whittaker") D = vegdist(decostand(Y,"total"),"manhattan")/2
   if(method=="percentagedifference") D = vegdist(Y, "bray")
   if(method=="wishart")   D = WishartD(Y)
  } else {
   if(method=="modmeanchardiff") D = D19(Y)
   if(method=="kulczynski")  D = vegdist(Y, "kulczynski")
   if(method=="ab.jaccard")  D = chao(Y, coeff="Jaccard", samp=samp)
   if(method=="ab.sorensen") D = chao(Y, coeff="Sorensen", samp=samp)
   if(method=="ab.ochiai")   D = chao(Y, coeff="Ochiai", samp=samp)
   if(method=="ab.simpson")  D = chao(Y, coeff="Simpson", samp=samp)
  }
  #
  if(sqrt.D) D = sqrt(D)
  SStotal <- sum(D^2)/n      # eq. 8
  BDtotal <- SStotal/(n-1)   # eq. 3
  delta1 <- centre(as.matrix(-0.5*D^2), n)   # eq. 9
  LCBD <- diag(delta1)/SStotal               # eq. 10b
  #
  out <- list(SStotal_BDtotal=c(SStotal,BDtotal), LCBD=LCBD,
              method=method, D=D)
 }
 ###
 ###
 method <- match.arg(method, c("euclidean", "manhattan", "modmeanchardiff",
"profiles", "hellinger", "chord", "chisquare", "divergence", "canberra", "whittaker",
"percentagedifference", "wishart", "kulczynski", "ab.jaccard",
"ab.sorensen","ab.ochiai","ab.simpson","jaccard","sorensen","ochiai","none"))
 #
 if(any(method == c("profiles", "hellinger", "chord", "chisquare", "manhattan",
"modmeanchardiff", "divergence", "canberra", "whittaker", "percentagedifference",
"kulczynski"))) require(vegan)
 if(any(method == c("jaccard","sorensen","ochiai"))) require(ade4)
 #
 if(is.table(Y)) Y <- Y[1:nrow(Y),1:ncol(Y)]    # In case class(Y) is "table"
 n <- nrow(Y)
 #
 aa <- system.time({
  if(any(method ==
```

```
        c("euclidean", "profiles", "hellinger", "chord", "chisquare","none"))) {
    note <- "Info -- This coefficient is Euclidean"
    res <- BD.group1(Y, method, save.D, per=FALSE)
    #
    # Permutation test for LCBD indices, distances group 1
    if(nperm>0) {
      p <- ncol(Y)
      nGE.L = rep(1,n)
      for(iperm in 1:nperm) {
        Y.perm = apply(Y,2,sample)
        res.p <- BD.group1(Y.perm, method, save.D, per=TRUE)
        ge <- which(res.p$LCBD >= res$LCBD)
nGE.L[ge] <- nGE.L[ge] + 1
      }
      p.LCBD <- nGE.L/(nperm+1)
} else { p.LCBD <- NA }
    #
    if(save.D) { D <- res$D } else { D <- NA }
#
    out <- list(SStotal_BDtotal=res$SStotal_BDtotal, SCBD=res$SCBD,
                LCBD=res$LCBD,    p.LCBD=p.LCBD,    method=method,    note=note,
D=D)
  } else {
    #
    if(method == "divergence") {
      note = "Info -- This coefficient is Euclidean"
    } else if(any(method == c("jaccard","sorensen","ochiai"))) {
      note = c("Info -- This coefficient is Euclidean because dist.binary ",
            "of ade4 computes it as sqrt(D). Use beta.div with option
sqrt.D=FALSE")
    } else if(any(method ==
c("manhattan","canberra","whittaker","percentagedifference","wishart"))) {
      if(sqrt.D) {
        note = "Info -- This coefficient, in the form sqrt(D), is Euclidean"
      } else {
        note = c("Info -- For this coefficient, sqrt(D) would be Euclidean",
              "Use is.euclid(D) of ade4 to check Euclideanarity of this D matrix")
      }
    } else {
      note = c("Info -- This coefficient is not Euclidean",
            "Use is.euclid(D) of ade4 to check Euclideanarity of this D matrix")
    }
```

```
    #
    res <- BD.group2(Y, method, sqrt.D)
    #
    # Permutation test for LCBD indices, distances group 2
    if(nperm>0) {
      nGE.L = rep(1,n)
      for(iperm in 1:nperm) {
        Y.perm = apply(Y,2,sample)
        res.p <- BD.group2(Y.perm, method, sqrt.D)
        ge <- which(res.p$LCBD >= res$LCBD)
nGE.L[ge] <- nGE.L[ge] + 1
      }
      p.LCBD <- nGE.L/(nperm+1)
} else { p.LCBD <- NA }
    #
    if(sqrt.D) note.sqrt.D<-"sqrt.D=TRUE"  else  note.sqrt.D<-"sqrt.D=FALSE"
if(save.D) { D <- res$D } else { D <- NA }
    #
    out <- list(SStotal_BDtotal=res$SStotal_BDtotal, LCBD=res$LCBD,
                p.LCBD=p.LCBD, method=c(method,note.sqrt.D), note=note, D=D)
  }
```

```
  #
  })
  aa[3] <- sprintf("%2f",aa[3])
  if(clock) cat("Time for computation =",aa[3]," sec\n")
  #
  class(out) <- "beta.div"
  out
}

D11 <- function(Y, algo=1)
  #
  # Compute Clark's coefficient of divergence.
  # Coefficient D11 in Legendre and Legendre (2012, eq. 7.51).
  #
  # License: GPL-2
  # Author:: Pierre Legendre, April 2011
{
  Y <- as.matrix(Y)
  n <- nrow(Y)
  p <- ncol(Y)
  # Prepare to divide by pp = (p-d) = no. species present at both sites
```

```
  Y.ap <- 1 - decostand(Y, "pa")
  d <- Y.ap %*% t(Y.ap)
  pp <- p-d   # n. species present at the two compared sites
  #
  if(algo==1) {   # Faster algorithm
    D <- matrix(0, n, n)
    for(i in 2:n) {
      for(j in 1:(i-1)) {
        num <- (Y[i,]-Y[j,])
        den <- (Y[i,]+Y[j,])
        sel <- which(den > 0)
        D[i,j] = sqrt(sum((num[sel]/den[sel])^2)/pp[i,j])
}
    }
    #
  } else {   # Slower algorithm
    D <- matrix(0, n, n)
    for(i in 2:n) {
      for(j in 1:(i-1)) {
        temp = 0
        for(p2 in 1:p) {
          den = Y[i,p2] + Y[j,p2]
          if(den > 0) {
            temp = temp + ((Y[i,p2] - Y[j,p2])/den)^2
          }
        }
        D[i,j] = sqrt(temp/pp[i,j])
      }
    }
    #
  }
  DD <- as.dist(D)
}

D19 <- function(Y)
  #
  # Compute the Modified mean character difference.
  # Coefficient D19 in Legendre and Legendre (2012, eq. 7.46).
  # Division is by pp = number of species present at the two compared sites
  #
  # License: GPL-2
  # Author:: Pierre Legendre, April 2011
```

```
{
 Y <- as.matrix(Y)
 n <- nrow(Y)
 p <- ncol(Y)
 # Prepare to divide by pp = (p-d) = n. species present at both sites
 Y.ap <- 1 - decostand(Y, "pa")
 d <- Y.ap %*% t(Y.ap)
 pp <- p-d   # n. species present at the two compared sites
 #
 D <- vegdist(Y, "manhattan")
 DD <- as.dist(as.matrix(D)/pp)
}

WishartD <- function(Y)
 #
 # Compute dissimilarity - 1 - Wishart similarity ratio (Wishart 1969).
 #
 # License: GPL-2
 # Author:: Pierre Legendre, August 2012
{
 CP = crossprod(t(Y))
 SS = apply(Y^2,1,sum)
 n = nrow(Y)
 mat.sq = matrix(0, n, n)
 for(i in 2:n) {
  for(j in 1:(n-1)) { mat.sq[i,j] = CP[i,j]/(SS[i] + SS[j] - CP[i,j]) }
 }
 mat = 1 - as.dist(mat.sq)
}

chao <- function(mat, coeff="Jaccard", samp=TRUE)
 #
 # Compute Chao et al. (2006) abundance-based indices.
 #
 # Arguments -
 # mat = data matrix, species abundances
 # coef = "Jaccard" : modified abundance-based Jaccard index
 #        "Sorensen": modified abundance-based Sørensen index
 #        "Ochiai"  : modified abundance-based Ochiai index
 #        "Simpson" : modified abundance-based Simpson index
 # samp=TRUE : Compute dissimilarities for sample data
 #     =FALSE: Compute dissimilarities for true population data
```

```
#
# Details -
# For coeff="Jaccard", the output values are identical to those
# produced by vegan's function vegdist(mat, "chao").
#
# Help received from A. Chao and T. C. Hsieh in July 2012 for the computation
# of dissimilarities for true population data is gratefully acknowledged.
#
# Reference --
# Chao, A., R. L. Chazdon, R. K. Colwell and T. J. Shen. 2006.
# Abundance-based similarity indices and their estimation when there
# are unseen species in samples. Biometrics 62: 361????"371.
#
# License: GPL-2
# Author:: Pierre Legendre, July 2012
{
 require(vegan)
 nn = nrow(mat)
 res = matrix(0,nn,nn)
 if(samp) {   # First for sample data
  for(k in 2:nn) {
for(j in 1:(k-1)) {
 #cat("k =",k,"  j =",j,"\n")
 v1 = mat[j,]   # Vector 1
 v2 = mat[k,]   # Vector 2
 v1.pa = decostand(v1,"pa")   # Vector 1 in presence-absence form
 v2.pa = decostand(v2,"pa")   # Vector 2 in presence-absence form
 N.j = sum(v1)   # Sum of abundances in vector 1
 N.k = sum(v2)   # Sum of abundances in vector 2
 shared.sp = v1.pa * v2.pa   # Vector of shared species ("pa")
 if(sum(shared.sp) == 0) {
  res[k,j] = 1
 } else {
  C.j = sum(shared.sp * v1)   # Sum of shared sp. abundances in v1
  C.k = sum(shared.sp * v2)   # Sum of shared sp. abundances in v2
  # a1.j = sum(shared.sp * v1.pa)
  # a1.k = sum(shared.sp * v2.pa)
  a1.j = length(which((shared.sp * v2) == 1)) # Singletons in v2
  a1.k = length(which((shared.sp * v1) == 1)) # Singletons in v1
  a2.j = length(which((shared.sp * v2) == 2)) # Doubletons in v2
  if(a2.j == 0) a2.j <- 1
  a2.k = length(which((shared.sp * v1) == 2)) # Doubletons in v1
```

```
if(a2.k == 0) a2.k <- 1
# S.j = sum(v1[which(v2 == 1)]) # Sum abund. in v1 for singletons in v2
# S.k = sum(v2[which(v1 == 1)]) # Sum abund. in v2 for singletons in v1
sel2 = which(v2 == 1)
sel1 = which(v1 == 1)
if(length(sel2)>0) S.j = sum(v1[sel2]) else S.j = 0
if(length(sel1)>0) S.k = sum(v2[sel1]) else S.k = 0

U.j = (C.j/N.j) + ((N.k-1)/N.k) * (a1.j/(2*a2.j)) * (S.j/N.j) # Eq. 11
if(U.j > 1) U.j <- 1
U.k = (C.k/N.k) + ((N.j-1)/N.j) * (a1.k/(2*a2.k)) * (S.k/N.k) # Eq. 12
if(U.k > 1) U.k <- 1

if(coeff == "Jaccard") {                    # "Jaccard"
  res[k,j] = 1 - (U.j*U.k/(U.j + U.k - U.j*U.k))
} else if(coeff == "Sorensen") {         # "Sorensen"
  res[k,j] = 1 - (2*U.j*U.k/(U.j + U.k))
} else if(coeff == "Ochiai") {           # "Ochiai"
  res[k,j] = 1 - (sqrt(U.j*U.k))
} else if(coeff == "Simpson") {
  # Simpson (1943), or Lennon et al. (2001) in Chao et al. (2006)
    res[k,j] = 1 -
     (U.j*U.k/(U.j*U.k+min((U.j-U.j*U.k),(U.k-U.j*U.k))))
   } else { #
    stop("Incorrect coefficient name")
   }
  }
 }
}
 } else {   # Now for complete population data
  for(k in 2:nn) {
 for(j in 1:(k-1)) {
  v1 = mat[j,]   # Vector 1
  v2 = mat[k,]   # Vector 2
  v1.pa = decostand(v1,"pa")   # Vector 1 in presence-absence form
  v2.pa = decostand(v2,"pa")   # Vector 2 in presence-absence form
  shared.sp = v1.pa * v2.pa    # Vector of shared species ("pa")
  if(sum(shared.sp) == 0) {
   res[k,j] = 1
  } else {
   N1 = sum(v1)   # Sum of abundances in vector 1
   N2 = sum(v2)   # Sum of abundances in vector 2
```

```
        U = sum(shared.sp * v1)/N1   # Sum of shared sp. abundances in v1
        V = sum(shared.sp * v2)/N2   # Sum of shared sp. abundances in v2


        if(coeff == "Jaccard") {                  # "Jaccard"
          res[k,j] = 1 - (U*V/(U + V - U*V))
} else if(coeff == "Sorensen") {         # "Sorensen"
          res[k,j] = 1 - (2*U*V/(U + V))
        } else if(coeff == "Ochiai") {           # "Ochiai"
res[k,j] = 1 - (sqrt(U*V))
} else if(coeff == "Simpson") { # "Simpson"
res[k,j] = 1 - (U*V/(U*V+min((U-U*V),(V-U*V)))) # Eq. ?
} else { #
          stop("Incorrect coefficient name")
         }
       }
     }
   }
 }
 res <- as.dist(res)
}
```



```
####end of beta.div Function

#### The following function applies beta.div to the list of matrices simulated under neutral dynamics. Arguments are: data, the list of matrices; dist, ecological distances as in the beta.div function (e.g. hellinger); n, number of simulated matrices (e.g. 4999) ###

BT_function<-function (data,dist,n)

 {

  beta_list<-vector('list',n)

  number<-1:n

    for(k in number) beta_list[[k]]<-beta.div(as.data.frame(data[[k]]),method=dist,nperm=0)[[1]][2]

    null<-unlist(beta_list)

  null

}

#### This functions calculated the lower and upper tail probability of the observed data relative to the null distribution of betadiversity of neutral matrices. Arguments are: null, the vector storing the estimate of beta diversity for neutral matrices; observed_data, observed beta diversity#

Test_Null_Function<-function (null,observed_beta)

   {

      count_vector<-vector('integer',length(null))

      number<-1:length(null)

            for(k in number) count_vector[[k]]<-ifelse(null[[k]]>observed_beta,1,0)

      P_2<-sum(unlist(count_vector))/length(null)
```

```
    P_1<-1-P_2

    results<-list(Prob_lowerTail=P_1,Prob_upper_Tail=P_2,Test=count_vector)

    results

   }

###This functions graph the null distribution and observed beta diversity

Graph_Null<-function (Null_Distr,Obs,color) {

hist(Null_Distr,xlab="Beta diversity",main="Null Distribution (bars) vs Observed value (vertica line)")

abline(v=Obs,col=color)

}

##############################END of Part 1####################

####################PART 2############################

######## Running the functions ######

#### set directory ####

####read the output from urn2.gp. Here it is assumed that in the working directory the urn2.gp output is called "simData.txt"###

simData<-read.table("simData.txt",blank.lines.skip=T,fill=T,flush=T)

##read the file containing the observed species by sites matrix. Here it is assumed that this file is called "observed.txt"###

obsData<-read.table("observed.txt")

###apply beta.div to observed data###

Observed_BT<-beta.div(obsData,method="hellinger",nperm=0)[[1]][2]

#### convert the output of urn2gp (Pari/Gp function) into a list of matrices. Here it is assumed that the number of sites in the observed and simulated data is "10"###

Neutral_Com<-listmatrix(simData,10,4999) # this may take several minutes

###apply beta.div to the list of matrices obtained with urn2gp

Null_vector<-BT_function(Neutral_Com,"hellinger",4999)

###Test

Null_Test<-Test_Null_Function(Null_vector,Observed_BT)

Null_Test[1]

Null_Test[2]

####Graphing

Graph_Null(Null_vector,Observed_BT,"red")
```

Example

There is an example for the procedure described in this paper which can be found here: http://onlinelibrary.wiley.com/doi/10.1002/ece3.1313/suppinfo. We do not show it here as it contains the information of 4999 simulated communities in a text-file which are based on the observed species matrix.

Appendix D. Supplementary Data for discussion: Co-occurrence analysis

In this analysis we used the software FORTRAN Pairs (Ulrich 2008) to explore if certain species pairs show non-random associations in terms of either segregation or aggregation using C-scores of a presence-absence matrix ('fixed-fixed': preserves row and column totals in random matrix). The C-score (Stone & Roberts 1990) measures the average number of 'checkerboard units' between all possible pairs of species (CU = $(r_i - S)$ $(r_j - S)$, with CU = checkerboard unit, S = n of shared sites (sites containing both species) and r_i and r_j = row totals for species i and j). Values above 2.0 or below -2.0, respectively, are significant at a probability of $p<0.05$. A positive value indicates that species segregate more often than expected by chance, a negative value indicates aggregation. For visualization, we show only species pairs which show at least one significant value in the different pooling options in at least one season(Table D 1). We tried different data pooling options to show that this might has strong effects on the outcome of the analysis. We not only show the analysis when the unit is based on the whole sample but also when the unit is the actual slice. Of special interest is at this point if there is a significant interaction after all, can this be observed in both seasons? Do closely related species segregate which would be expected by the limiting similarity concept? As it becomes clear in Table D 1, there are several species pairs which show significant C-scores in both seasons. When we looked at the original data, most of these significant values proved to be statistical artifacts, mostly due to too low abundances of one or both of the species. However, the analysis reveals that it is a general useful tool to detect species pairs which might be interesting for further analysis in terms of competition but needs further replication.

Table D 1 Summary of species pairs which show at least one significant C-score in at least one season.Analyses are based on 'whole sample' (all slices pooled) or 'slice' where slices are treated independently as samples. u= uphill subplots only, d = downhill subplots only, u + d = up- and downhill subplots pooled. Values higher than 2.0 or lower -2.0, indicating significant relationships, are highlighted in grey.

		macroplot	**1 + 2**						**1**						**2**					
		location	**u + d**	**u + d**	**u**	**u**	**d**	**d**	**u + d**	**u + d**	**u**	**u**	**d**	**d**	**u + d**	**u + d**	**u**	**u**	**d**	**d**
		based on	**sample**	**slice**	**sample**	**slice**	**sample**	**slice**	**sample**	**slice**	**sample**	**slice**	**sample**	**slice**	**sample**	**slice**	**sample**	**slice**	**sample**	**slice**
season	**species1**	**species2**																		
May 2012	*A. coleoptrata*	*S. sculptus*	0.40	0.31	0.50	0.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oct 2012	*A. coleoptrata*	*S. sculptus*	-1.28	0.47	0.00	0.00	-2.13	0.39	-1.42	0.37	0.00	0.00	-1.02	0.58	0.00	0.00	0.00	0.00	0.00	0.00
May 2012	*A. coleoptrata*	*T. incisellus*	-2.13	0.31	0.00	0.00	-1.49	0.40	-2.21	0.31	0.00	0.00	-1.46	0.55	0.00	0.00	0.00	0.00	0.00	0.00
Oct 2012	*A. coleoptrata*	*T. incisellus*	0.94	0.67	1.15	0.78	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.02	0.85	1.06	0.72	0.00	0.00
May 2012	*C. birulai*	*P. phaenotus*	-1.06	1.80	-1.00	2.07	0.00	0.00	-0.93	1.68	-0.60	1.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oct 2012	*C. birulai*	*P. phaenotus*	-0.29	1.20	-0.29	0.00	0.00	0.00	-0.25	1.28	0.00	1.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
May 2012	*C. birulai*	*P. punctum*	-0.72	1.22	-0.65	2.02	0.00	0.00	-0.61	1.37	-1.08	1.05	0.00	0.00	0.00	0.00	0.00	0.00	-0.75	-1.00
Oct 2012	*C. birulai*	*P. punctum*	-0.44	0.96	-0.18	0.00	0.00	0.00	-0.48	0.82	-0.35	0.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
May 2012	*C. birulai*	*R. ardua*	0.79	0.48	0.71	0.67	0.00	0.00	0.78	0.41	1.51	0.68	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oct 2012	*C. birulai*	*R. ardua*	-3.00	0.25	-2.59	0.00	0.00	0.00	-1.46	0.33	-1.42	0.42	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
May 2012	*C. birulai*	*T. vel. sarekensis*	1.13	1.23	0.17	0.93	0.00	0.00	0.84	1.29	0.52	1.16	0.00	0.00	0.00	0.00	0.00	0.00	-3.00	-4.90
Oct 2012	*C. birulai*	*T. vel. sarekensis*	-0.67	0.62	-0.70	0.00	0.00	0.00	-0.55	0.70	-0.47	1.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
May 2012	*D. ornata*	*E. occultus*	0.00	0.00	-0.62	-0.47	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.61	0.58	2.02	1.04	0.00	0.00
Oct 2012	*D. ornata*	*E. occultus*	-0.82	0.08	-0.42	-0.59	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-1.55	-0.42	-1.21	0.83	0.00	0.00
May 2012	*D. ornata*	*L. coracinus*	0.00	0.00	-1.45	-2.54	0.55	0.48	0.00	0.00	0.00	0.00	0.00	0.00	1.01	-0.88	1.81	-1.06	0.00	0.00
Oct 2012	*D. ornata*	*L. coracinus*	-1.38	-1.10	-1.54	-0.61	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-1.10	-0.64	-0.45	0.66	0.00	0.16
May 2012	*D. ornata*	*M. minus*	0.00	0.00	-1.92	-2.94	-1.10	0.32	0.00	0.00	0.00	0.00	0.00	0.00	-1.33	-0.82	-1.52	-1.50	0.00	0.00
Oct 2012	*D. ornata*	*M. minus*	-0.36	-0.37	-0.40	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-0.88	-0.92	-0.91	-0.65	0.00	0.00
May 2012	*D. ornata*	*O. nova*	0.00	0.00	-1.36	-2.01	-1.47	-1.38	0.00	0.00	0.00	0.00	0.00	0.00	-0.03	-0.83	1.05	-0.80	0.00	0.00
Oct 2012	*D. ornata*	*O. nova*	-2.13	-1.94	-1.55	-1.37	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-1.79	-1.43	-1.26	-0.30	0.00	0.00
May 2012	*D. ornata*	*P. capucinus*	0.00	0.00	2.50	1.51	0.95	0.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Oct 2012	*D. ornata*	*P. capucinus*	1.82	1.63	2.07	2.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.46	1.17	1.04	0.85	0.00	0.00
May 2012	*D. ornata*	*P. spinosa*	0.00	0.00	-0.82	-2.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.28	-1.05	1.61	-1.11	-1.01	-0.14
Oct 2012	*D. ornata*	*P. spinosa*	-1.67	-1.96	-1.12	-1.57	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-1.23	-1.53	-0.60	-0.89	0.00	0.00
May 2012	*D. ornata*	*P. phaenotus*	0.00	0.00	1.56	0.20	0.37	3.36	0.00	0.00	0.00	0.00	0.00	0.00	2.07	2.50	0.30	0.09	0.00	0.00
Oct 2012	*D. ornata*	*P. phaenotus*	-0.91	-0.53	-0.56	-0.48	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-0.95	-0.60	-1.11	-0.05	0.00	0.00
May 2012	*D. ornata*	*R. ardua*	0.00	0.00	2.32	1.41	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oct 2012	*D. ornata*	*R. ardua*	0.85	0.90	0.98	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
May 2012	*D. ornata*	*S. sarekensis*	0.00	0.00	-1.82	-2.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-1.23	-1.50	-1.09	-1.25	0.00	0.00
Oct 2012	*D. ornata*	*S. sarekensis*	-0.36	-0.92	-1.13	-0.94	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.14	-0.35	-0.50	-0.99	0.00	0.00
May 2012	*D. ornata*	*T. incisellus*	0.00	0.00	-0.07	0.08	0.13	1.22	0.00	0.00	0.00	0.00	0.00	0.00	1.47	2.06	2.76	1.49	0.00	0.00
Oct 2012	*D. ornata*	*T. incisellus*	-0.77	-0.55	-0.16	-0.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-1.00	-0.43	-0.57	0.81	0.00	0.00
May 2012	*E. occultus*	*E. tardus*	0.00	0.00	1.15	1.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.71	1.35	1.84	2.37	0.00	0.00
Oct 2012	*E. occultus*	*E. tardus*	-0.75	0.76	-0.51	0.21	0.00	0.00	-1.04	-0.75	-1.13	-0.95	0.00	0.00	-0.85	0.84	-0.40	-0.35	0.00	0.00
May 2012	*E. occultus*	*L. coracinus*	0.00	0.00	-2.32	-2.80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-2.12	-2.03	-1.41	-1.63	0.00	0.00
Oct 2012	*E. occultus*	*L. coracinus*	-0.45	-0.62	-0.48	-1.80	0.00	0.00	1.23	0.73	0.00	0.00	0.00	0.00	-1.73	-1.62	-1.30	-1.18	-1.17	0.81
May 2012	*E. occultus*	*L. pannonica*	0.00	0.00	-1.67	-1.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-0.70	-0.34	0.00	-0.28	0.00	0.00
Oct 2012	*E. occultus*	*L. pannonica*	2.52	0.83	0.85	-0.93	0.00	0.00	2.42	0.35	0.41	-1.10	0.00	0.00	0.00	-0.54	0.00	-0.40	-0.39	-0.98
May 2012	*E. occultus*	*M. minus*	0.00	0.00	-0.97	-0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.46	1.34	0.76	2.12	0.00	0.00
Oct 2012	*E. occultus*	*M. minus*	1.51	2.17	1.95	0.22	0.00	0.00	2.06	2.45	2.84	3.04	0.00	0.00	-0.11	-0.23	-0.28	0.89	0.00	0.00
May 2012	*E. occultus*	*O. nova*	0.00	0.00	-2.18	-2.16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-1.92	-1.56	-1.28	-0.77	0.00	0.00
Oct 2012	*E. occultus*	*O. nova*	-1.20	-1.25	-0.45	-1.39	0.00	0.00	-1.06	-2.00	-0.74	-1.47	0.00	0.00	-1.23	-1.04	-0.54	-0.53	0.00	0.00
May 2012	*E. occultus*	*P. capucinus*	0.00	0.00	1.93	1.74	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oct 2012	*E. occultus*	*P. capucinus*	-0.36	2.04	0.06	1.21	0.00	0.00	-0.23	1.51	0.58	2.25	0.00	0.00	0.73	0.65	0.48	0.37	0.00	0.00
May 2012	*E. occultus*	*P. spinosa*	0.00	0.00	-1.53	-2.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-1.69	-1.73	-0.94	-1.03	0.00	0.00
Oct 2012	*E. occultus*	*P. spinosa*	-1.16	-1.42	-0.72	-0.24	0.00	0.00	-1.63	-2.54	-1.39	-2.08	0.00	0.00	0.23	-0.09	0.88	1.11	0.00	0.00
May 2012	*E. occultus*	*R. ardua*	0.00	0.00	1.49	1.39	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oct 2012	*E. occultus*	*R. ardua*	-2.08	-1.71	-1.41	0.00	0.00	0.00	-1.32	-2.11	-1.02	-1.41	0.00	0.00	0.00	0.00	0.00	0.00	1.94	2.66
May 2012	*E. occultus*	*S. quintus*	0.00	0.00	-1.14	-0.86	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-1.05	-0.65	-1.04	-0.10	0.00	0.00
Oct 2012	*E. occultus*	*S. quintus*	-1.61	-1.99	-1.83	-1.50	0.00	0.00	-1.65	-2.40	-1.47	-2.23	0.00	0.00	-0.69	-0.86	-1.09	-0.85	0.00	0.00

May 2012	*E. occultus*	*S. sarekensis*	0.00	0.00	-1.93	-1.37	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-1.80	-0.87	-1.37	-0.45	0.00	0.00
Oct 2012	*E. occultus*	*S. sarekensis*	2.28	1.80	1.69	0.83	0.00	0.00	1.31	0.86	1.28	0.64	0.00	0.00	1.64	1.05	1.12	0.59	0.00	0.00
May 2012	*E. occultus*	*T. incisellus*	0.00	0.00	-1.45	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-0.47	0.98	0.08	1.61	0.00	0.00
Oct 2012	*E. occultus*	*T. incisellus*	-2.31	-2.24	-1.84	-1.82	0.00	0.00	-1.54	-2.32	-1.26	-2.00	0.00	0.00	-1.34	-1.80	-1.16	-1.33	0.00	0.00
May 2012	*E. occultus*	*T. vel. sarekensis*	0.00	0.00	3.13	1.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.35	2.24	2.37	0.97	-0.56	-0.67
Oct 2012	*E. occultus*	*T. vel. sarekensis*	-0.43	-0.70	-0.21	1.45	0.00	0.00	-1.42	-1.66	-0.94	-1.50	0.00	0.00	2.07	1.57	1.69	1.08	0.00	0.00
May 2012	*E. cylindrica*	*L. pannonica*	1.27	0.41	1.59	1.33	0.00	0.00	0.99	0.48	-0.22	-0.59	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oct 2012	*E. cylindrica*	*L. pannonica*	5.18	2.12	2.22	1.25	0.00	0.00	3.54	1.80	0.84	1.36	0.00	0.00	0.00	0.00	0.00	0.00	-1.13	-1.25
May 2012	*E. cylindrica*	*M. minus*	0.44	0.40	1.54	1.65	0.00	0.00	0.48	0.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oct 2012	*E. cylindrica*	*M. minus*	0.93	1.53	0.92	1.33	0.00	0.00	1.58	1.61	1.53	2.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
May 2012	*E. cylindrica*	*O. nova*	0.00	0.00	1.79	1.84	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oct 2012	*E. cylindrica*	*O. nova*	1.74	1.01	2.73	1.00	0.00	0.00	1.32	0.78	2.02	1.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
May 2012	*E. cylindrica*	*P. capucinus*	-1.82	-1.07	-2.12	-1.00	0.00	0.00	-2.06	-1.05	-1.29	-0.69	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oct 2012	*E. cylindrica*	*P. capucinus*	-1.32	-0.68	-1.25	0.72	0.00	0.00	-0.72	-0.30	-0.19	0.37	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
May 2012	*E. cylindrica*	*P. nervosa*	1.25	1.12	2.02	1.43	0.00	0.00	1.08	1.08	2.13	1.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oct 2012	*E. cylindrica*	*P. nervosa*	2.10	1.76	2.40	1.25	0.00	0.00	1.86	1.51	3.15	2.02	0.00	0.00	0.00	0.00	0.00	0.00	0.27	0.25
May 2012	*E. cylindrica*	*P. phaenotus*	1.81	2.70	1.70	2.83	0.00	0.00	2.02	3.03	2.77	3.28	0.00	0.00	0.00	0.00	0.00	0.00	0.59	0.37
Oct 2012	*E. cylindrica*	*P. phaenotus*	-0.68	1.99	-0.37	1.36	0.00	0.00	-0.48	2.39	0.00	2.82	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
May 2012	*E. cylindrica*	*P. punctum*	2.40	2.05	1.97	3.21	0.00	0.00	2.47	2.22	1.17	2.06	0.00	0.00	0.00	0.00	0.00	0.00	0.47	-1.93
Oct 2012	*E. cylindrica*	*P. punctum*	0.61	1.80	1.83	1.49	0.00	0.00	0.09	1.48	1.19	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
May 2012	*E. cylindrica*	*S. laevigatus*	1.04	1.77	1.65	2.45	0.00	0.00	0.69	1.70	2.51	2.46	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oct 2012	*E. cylindrica*	*S. laevigatus*	-1.65	1.17	-1.13	1.00	0.00	0.00	-1.06	1.71	0.00	2.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
May 2012	*E. cylindrica*	*T. vel. alatus*	-2.13	-2.38	-1.94	-2.59	0.00	0.00	-1.88	-3.39	-1.25	-2.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oct 2012	*E. cylindrica*	*T. vel. alatus*	-2.00	0.33	-2.59	0.00	0.00	0.00	-1.56	0.42	-1.11	0.59	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
May 2012	*E. cylindrica*	*T. vel. sarekensis*	0.26	1.98	-0.27	1.78	0.00	0.00	0.49	2.35	0.20	1.61	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oct 2012	*E. cylindrica*	*T. vel. sarekensis*	-1.41	1.49	-1.11	0.77	0.00	0.00	-1.12	1.42	-0.97	2.00	0.00	0.00	0.00	0.00	0.00	0.00	-0.75	0.64
May 2012	*E. tardus*	*M. minus*	0.35	0.23	-2.05	-1.76	0.00	0.00	0.33	0.18	0.00	0.00	0.00	0.00	-1.53	-1.79	-1.48	-1.68	0.00	0.00
Oct 2012	*E. tardus*	*M. minus*	1.43	2.39	1.80	2.40	-0.56	1.15	3.18	1.61	2.68	1.60	0.58	0.53	-0.97	1.23	-0.73	0.55	0.00	0.00
May 2012	*E. tardus*	*P. capucinus*	1.25	0.69	2.08	1.34	0.00	0.00	1.13	0.76	2.04	0.77	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Oct 2012	*E. tardus*	*P. capucinus*	1.26	2.83	1.91	3.48	0.40	0.39	0.58	1.19	0.60	1.25	0.00	0.00	0.72	1.92	-0.27	2.59	0.00	0.00
May 2012	*E. tardus*	*P. spinosa*	-2.59	0.18	-1.12	-1.64	0.00	0.00	-3.18	0.23	-1.69	0.35	0.00	0.00	-1.28	-1.79	-0.27	-1.26	0.00	0.00
Oct 2012	*E. tardus*	*P. spinosa*	-1.66	-1.38	-1.64	-1.63	0.45	0.44	-0.26	-1.22	-0.51	-1.37	0.00	0.00	-1.62	-0.82	-1.42	-1.21	0.00	0.00
May 2012	*E. tardus*	*P. phaenotus*	-0.79	-1.29	1.64	0.77	0.00	0.00	-0.78	-1.15	-0.62	-1.21	0.00	0.00	3.96	3.08	2.17	2.97	0.00	0.00
Oct 2012	*E. tardus*	*P. phaenotus*	-0.76	0.18	1.20	-0.18	-1.04	-0.10	-0.53	1.05	0.00	0.43	-0.83	0.90	-0.91	-0.36	0.42	-0.67	0.00	0.00
May 2012	*E. tardus*	*S. laevigatus*	-1.20	-1.93	1.22	-0.41	0.00	0.00	-1.40	-1.93	-0.59	-1.47	0.00	0.00	1.25	0.36	1.39	0.38	0.00	0.00
Oct 2012	*E. tardus*	*S. laevigatus*	0.35	1.01	2.37	1.90	0.00	0.00	0.00	-0.05	0.00	0.26	0.00	0.00	-1.18	-0.40	-0.73	-0.72	0.00	0.00
May 2012	*E. tardus*	*T. incisellus*	0.62	0.45	0.63	1.42	0.00	0.00	0.66	0.50	0.00	0.00	0.00	0.00	0.86	1.67	1.55	2.12	0.00	0.00
Oct 2012	*E. tardus*	*T. incisellus*	-0.36	0.30	-0.32	0.26	0.64	0.50	-0.64	-0.47	-1.18	-0.73	0.29	0.23	-0.13	0.53	1.18	0.52	0.00	0.00
May 2012	*E. tardus*	*T. vel. sarekensis*	-0.60	-1.56	-0.79	-0.25	0.00	0.00	-0.81	-1.69	-1.06	-1.92	0.00	0.00	0.35	2.30	-0.47	1.64	0.00	0.00
Oct 2012	*E. tardus*	*T. vel. sarekensis*	-0.09	-0.02	0.80	-0.19	-1.35	-0.76	-0.15	-0.01	-0.71	-0.18	0.42	0.31	-0.90	-0.16	1.18	0.15	0.00	0.00
May 2012	*L. coracinus*	*L. pannonica*	0.00	0.00	-1.71	-2.99	-0.31	-0.83	0.00	0.00	0.00	0.00	0.00	0.00	-0.91	-2.07	0.00	-1.68	0.00	0.00
Oct 2012	*L. coracinus*	*L. pannonica*	-0.66	-2.16	-1.32	-1.57	0.00	-1.12	-0.48	-1.40	0.00	0.00	0.00	-1.22	0.00	-1.12	0.00	-1.03	0.00	0.00
May 2012	*L. coracinus*	*O. nova*	0.00	0.00	-2.01	-3.00	-4.90	-3.00	0.00	0.00	0.00	0.00	0.00	0.00	-1.70	-2.45	-1.62	-2.17	-0.35	-1.45
Oct 2012	*L. coracinus*	*O. nova*	-0.98	-1.63	-0.89	-1.40	0.00	0.00	1.21	0.47	0.00	0.00	0.00	0.00	-1.20	-1.21	-0.07	-0.18	0.00	0.00
May 2012	*L. coracinus*	*P. capucinus*	0.00	0.00	2.63	1.55	0.35	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oct 2012	*L. coracinus*	*P. capucinus*	0.88	1.57	0.67	2.32	0.37	0.25	1.66	0.90	0.00	0.00	0.00	0.00	-0.71	1.02	-0.72	0.87	0.00	0.00
May 2012	*L. coracinus*	*P. nervosa*	0.00	0.00	-0.88	-1.73	0.20	0.20	0.00	0.00	0.00	0.00	0.00	0.00	-1.69	-2.05	-1.31	-1.53	0.00	-0.72
Oct 2012	*L. coracinus*	*P. nervosa*	0.34	-0.81	-0.29	-0.82	0.04	-0.25	0.84	-0.37	0.00	0.00	-0.75	-1.42	0.14	-0.06	-0.62	-0.38	0.56	0.40
May 2012	*L. coracinus*	*P. spinosa*	0.00	0.00	-1.68	-2.77	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-1.87	-2.59	-1.28	-2.09	0.00	0.00
Oct 2012	*L. coracinus*	*P. spinosa*	-0.17	-0.78	-0.12	-0.94	0.35	0.27	0.96	0.52	0.00	0.00	0.00	0.00	-0.55	-0.75	0.78	0.20	1.53	1.42
May 2012	*L. coracinus*	*P. punctum*	0.00	0.00	-1.46	-2.57	-0.20	-0.67	0.00	0.00	0.00	0.00	0.00	0.00	-0.79	-2.39	-1.42	-1.51	-1.04	-1.46
Oct 2012	*L. coracinus*	*P. punctum*	-0.29	-0.75	-0.70	-1.33	-0.09	1.21	0.70	1.27	0.00	0.00	-1.38	0.54	-0.62	-1.12	0.00	-0.99	-0.45	-0.72
May 2012	*L. coracinus*	*R. ardua*	0.00	0.00	2.14	1.49	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.23	0.25
Oct 2012	*L. coracinus*	*R. ardua*	0.94	0.86	1.09	0.00	0.00	0.00	0.93	0.51	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-0.78	-1.20
May 2012	*L. coracinus*	*S. sarekensis*	0.00	0.00	-1.72	-2.42	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-1.44	-1.79	-0.96	-1.18	-0.52	-1.02
Oct 2012	*L. coracinus*	*S. sarekensis*	0.02	-0.72	-0.97	-1.03	0.87	0.56	0.73	0.50	0.00	0.00	0.40	0.35	-0.04	-0.35	-0.49	-1.11	0.78	0.42
May 2012	*L. coracinus*	*T. incisellus*	0.00	0.00	-2.03	0.20	0.59	0.45	-1.33	0.00	0.00	0.00	0.00	0.00	-0.51	1.22	-0.53	1.82	0.40	0.29
Oct 2012	*L. coracinus*	*T. incisellus*	0.04	-0.98	-0.26	-1.18	0.45	0.42	1.63	0.85	0.00	0.00	0.37	0.33	-0.97	-1.26	-0.41	-0.59	0.64	0.44

May 2012	*L. coracinus*	*T. vel. sarekensis*	0.00	0.00	4.57	1.04	-0.52	-0.85	0.00	0.00	0.00	0.00	0.00	0.00	3.91	1.12	3.15	1.03	-0.48	-0.92
Oct 2012	*L. coracinus*	*T. vel. sarekensis*	1.85	0.40	3.08	1.02	-0.84	-1.50	0.52	-0.29	0.00	0.00	-1.64	-2.00	1.53	1.30	2.91	1.40	0.00	0.00
May 2012	*L. pannonica*	*M. minus*	-0.89	0.72	-1.57	-1.52	-0.87	0.75	-0.67	0.69	0.00	0.00	0.00	1.28	-0.94	-0.34	0.00	-0.13	0.00	0.00
Oct 2012	*L. pannonica*	*M. minus*	1.96	4.20	0.75	2.18	0.00	1.89	1.42	3.16	0.39	3.77	0.00	0.36	0.00	1.54	0.00	0.24	0.00	0.00
May 2012	*L. pannonica*	*O. nova*	0.00	0.00	-2.08	-2.39	-0.53	-1.37	0.00	0.00	0.00	0.00	0.00	0.00	-1.03	-1.34	0.00	-1.16	-0.45	-1.15
Oct 2012	*L. pannonica*	*O. nova*	0.19	-1.48	-1.38	-2.00	0.00	0.00	1.23	-0.47	-0.32	-1.77	0.00	0.00	0.00	-0.88	0.00	-1.00	0.00	0.00
May 2012	*L. pannonica*	*P. capucinus*	1.32	1.25	3.02	1.89	-0.45	2.22	1.33	1.24	0.73	-0.10	0.00	1.81	0.00	0.00	0.00	0.00	0.00	-0.67
Oct 2012	*L. pannonica*	*P. capucinus*	2.83	3.64	1.03	4.37	0.00	-0.72	1.98	3.15	-0.19	2.59	0.00	0.00	0.00	1.60	0.00	2.00	0.00	0.00
May 2012	*L. pannonica*	*P. spinosa*	-0.82	0.73	-1.99	-2.33	0.00	0.00	-0.73	0.61	-1.56	0.47	0.00	0.00	-0.71	-1.80	0.00	-1.44	0.00	-1.24
Oct 2012	*L. pannonica*	*P. spinosa*	1.99	-1.27	-0.20	-1.85	0.00	-0.83	3.38	0.76	1.29	-0.36	0.00	0.00	0.00	-1.39	0.00	-1.18	1.46	1.28
May 2012	*L. pannonica*	*R. ardua*	1.80	1.57	2.40	2.60	0.00	0.00	2.06	1.51	0.18	1.16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-0.59
Oct 2012	*L. pannonica*	*R. ardua*	2.59	2.35	1.35	0.00	0.00	0.00	2.48	2.09	0.51	1.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
May 2012	*L. pannonica*	*S. laevigatus*	5.64	1.78	1.66	1.82	-0.70	-0.12	2.29	2.07	0.56	1.13	0.00	0.31	-0.90	-0.59	0.00	0.00	0.00	-1.86
Oct 2012	*L. pannonica*	*S. laevigatus*	4.62	0.46	2.15	-0.25	0.00	0.00	4.23	-0.22	0.00	-2.06	0.00	0.00	0.00	-0.87	0.00	-0.91	-0.61	-0.54
May 2012	*L. pannonica*	*S. quintus*	1.98	0.33	0.45	-1.44	-0.61	-0.80	2.13	0.22	1.72	0.84	0.00	-0.89	-0.77	-1.73	0.00	-1.62	0.00	-0.51
Oct 2012	*L. pannonica*	*S. quintus*	0.28	-1.78	-0.10	-0.68	0.00	-2.52	1.92	-0.42	0.44	-0.84	0.00	-1.22	0.00	-1.26	0.00	0.66	0.00	0.00
May 2012	*L. pannonica*	*T. vel. sarekensis*	-1.17	-1.84	0.26	1.02	-0.99	-1.20	-1.63	-1.93	-1.16	-1.29	0.00	-0.72	0.07	0.68	0.00	1.28	0.00	0.00
Oct 2012	*L. pannonica*	*T. vel. sarekensis*	2.40	0.69	1.43	0.19	0.00	0.01	3.17	0.02	1.25	-0.71	0.00	-1.39	0.00	1.24	0.00	-0.09	0.74	-0.19
May 2012	*M. minus*	*O. nova*	0.00	0.00	-1.96	-1.45	-0.80	-0.70	0.00	0.00	0.00	0.00	0.00	0.00	-0.37	0.23	-0.38	0.55	0.00	0.00
Oct 2012	*M. minus*	*O. nova*	-0.13	0.17	-0.38	-0.10	0.00	0.00	0.00	1.74	-0.01	2.04	0.00	0.00	-0.75	-1.21	-0.95	-1.22	-0.45	-0.36
May 2012	*M. minus*	*P. capucinus*	-1.33	0.56	2.25	2.11	-0.75	0.85	-1.28	0.62	0.00	0.00	-1.69	0.48	0.00	0.00	0.00	0.00	1.53	1.01
Oct 2012	*M. minus*	*P. capucinus*	1.62	1.50	1.12	1.28	0.65	0.55	1.59	1.29	1.95	1.87	0.00	0.00	1.44	1.23	0.92	0.70	-0.94	1.54
May 2012	*M. minus*	*P. phaenotus*	-0.50	1.39	1.81	1.43	-0.01	1.92	-0.58	1.02	0.00	0.00	-0.67	1.53	2.37	1.50	1.00	1.28	0.00	0.00
Oct 2012	*M. minus*	*P. phaenotus*	0.98	6.24	0.98	4.94	0.50	2.23	1.02	5.56	0.00	6.12	1.26	1.26	0.15	1.70	1.18	1.05	0.00	0.00
May 2012	*M. minus*	*P. punctum*	-0.48	1.00	-0.42	0.86	-0.40	1.76	-0.47	0.94	0.00	0.00	0.00	1.60	0.30	1.94	1.06	2.15	0.00	0.00
Oct 2012	*M. minus*	*P. punctum*	1.64	4.29	1.70	2.89	0.48	2.64	0.32	3.82	1.86	5.15	-0.86	0.79	1.16	1.80	0.00	0.70	-0.64	-1.11
May 2012	*M. minus*	*R. ardua*	0.59	0.39	1.73	1.70	0.00	0.00	0.44	0.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.62	1.74
Oct 2012	*M. minus*	*R. ardua*	1.60	1.48	1.74	0.00	0.00	0.00	2.63	1.97	3.26	2.28	0.00	0.00	0.00	0.00	0.00	0.00	-0.77	1.53
May 2012	*M. minus*	*S. laevigatus*	1.11	0.83	2.68	2.15	0.24	1.75	1.11	0.75	0.00	0.00	0.52	0.55	1.77	1.65	1.57	1.00	-0.99	0.23

Oct 2012	*M. minus*	*S. laevigatus*	-1.80	0.39	-1.94	0.23	0.00	0.00	-0.64	2.13	0.00	3.13	0.00	0.00	-1.76	-1.81	-1.43	-1.53	0.00	0.00
May 2012	*M. minus*	*S. quintus*	0.53	0.31	-0.42	0.78	-0.07	1.39	0.70	0.25	0.00	0.00	0.31	0.29	0.65	2.58	-0.18	1.71	0.00	0.00
Oct 2012	*M. minus*	*S. quintus*	3.21	4.74	2.20	3.27	0.42	1.95	2.83	2.89	3.30	2.92	0.70	0.56	0.79	3.71	0.64	3.55	1.24	0.99
May 2012	*M. minus*	*S. sarekensis*	0.00	0.00	-2.10	-1.94	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-1.18	-0.81	-1.23	-0.70	0.00	0.00
Oct 2012	*M. minus*	*S. sarekensis*	3.58	2.12	1.61	1.61	1.40	1.21	2.41	1.70	1.56	1.11	0.53	0.50	2.21	1.10	0.35	0.17	0.00	0.00
May 2012	*M. minus*	*T. incisellus*	-2.00	0.37	0.69	2.17	0.29	1.44	-2.29	0.20	0.00	0.00	-1.42	0.52	4.03	4.05	3.58	4.20	0.00	0.00
Oct 2012	*M. minus*	*T. incisellus*	2.28	2.72	2.39	1.39	1.07	0.80	3.14	2.88	4.64	3.08	0.55	0.50	0.42	0.10	-0.05	0.68	0.00	0.00
May 2012	*M. minus*	*T. vel. sarekensis*	-0.58	0.90	0.46	0.96	-1.09	1.06	-0.58	0.80	0.00	0.00	-0.33	1.69	-0.83	1.26	-0.61	0.37	0.64	0.47
Oct 2012	*M. minus*	*T. vel. sarekensis*	0.93	2.26	0.25	2.02	0.50	-0.15	0.88	3.47	0.74	3.63	0.77	1.01	0.11	-0.23	0.11	-0.04	-0.53	-1.30
May 2012	*O. nova*	*P. capucinus*	0.00	0.00	2.73	2.39	0.50	0.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.55
Oct 2012	*O. nova*	*P. capucinus*	3.13	2.36	5.35	3.31	0.00	0.00	2.03	1.30	3.28	1.80	0.00	0.00	2.08	2.19	2.38	1.83	0.00	0.00
May 2012	*O. nova*	*P. nervosa*	0.00	0.00	-0.69	-1.69	0.37	0.25	0.00	0.00	0.00	0.00	0.00	0.00	-1.49	-2.28	-0.98	-1.78	0.80	-0.20
Oct 2012	*O. nova*	*P. nervosa*	-0.48	-1.41	-0.58	-0.57	0.00	0.00	-1.05	-1.83	-0.66	-1.75	0.00	0.00	0.34	0.49	-0.73	-0.23	0.00	0.00
May 2012	*O. nova*	*P. spinosa*	0.00	0.00	-2.33	-2.90	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-2.03	-2.53	-1.46	-1.96	0.00	0.00
Oct 2012	*O. nova*	*P. spinosa*	-1.54	-2.15	-0.87	-1.27	0.00	0.00	-1.48	-2.33	-1.01	-1.96	0.00	0.00	-0.76	-1.04	1.16	0.14	0.00	0.00
May 2012	*O. nova*	*R. ardua*	0.00	0.00	2.55	1.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oct 2012	*O. nova*	*R. ardua*	-0.24	-0.09	0.33	0.00	0.00	0.00	-0.58	-1.13	-0.38	-0.80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
May 2012	*O. nova*	*S. quintus*	0.00	0.00	-1.34	-0.93	0.59	0.44	0.00	0.00	0.00	0.00	0.00	0.00	-0.27	0.30	-1.05	-0.02	0.00	0.00
Oct 2012	*O. nova*	*S. quintus*	0.44	-0.02	-0.19	0.14	0.00	0.00	-0.80	-1.61	-0.70	-1.72	0.00	0.00	2.52	3.08	1.38	3.58	0.00	0.00
May 2012	*O. nova*	*S. sarekensis*	0.00	0.00	-1.76	-2.65	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-1.23	-2.14	-0.86	-1.79	0.00	0.00
Oct 2012	*O. nova*	*S. sarekensis*	1.14	0.24	0.34	-0.19	0.00	0.00	1.15	0.55	0.80	0.52	0.00	0.00	1.34	0.62	0.74	0.35	0.00	0.00
May 2012	*O. nova*	*T. incisellus*	0.00	0.00	-1.73	-0.25	1.02	0.74	0.00	0.00	0.00	0.00	0.00	0.00	0.09	1.27	-0.04	1.77	0.00	0.00
Oct 2012	*O. nova*	*T. incisellus*	-1.51	-2.22	-1.00	-1.49	0.00	0.00	-0.59	-1.57	-0.28	-1.45	0.00	0.00	-1.66	-1.66	-1.16	-0.91	0.00	0.00
May 2012	*O. nova*	*T. vel. sarekensis*	0.00	0.00	2.84	2.10	1.25	0.03	0.00	0.00	0.00	0.00	0.00	0.00	4.07	2.73	2.38	1.78	-1.08	0.59
Oct 2012	*O. nova*	*T. vel. sarekensis*	-0.60	-0.79	-0.03	0.14	0.00	0.00	-1.12	-2.12	-1.07	-1.62	0.00	0.00	-0.16	0.52	0.16	0.65	-1.88	0.27
May 2012	*P. perforatus*	*P. phaenotus*	0.85	0.30	-0.67	-0.80	2.59	1.49	0.67	0.31	-0.42	-1.04	1.33	1.83	0.00	0.00	0.00	0.00	0.00	0.00
Oct 2012	*P. perforatus*	*P. phaenotus*	2.84	1.90	0.00	0.00	1.46	1.63	3.39	2.02	0.00	0.00	1.49	1.15	0.00	0.00	0.00	0.00	0.00	0.00
May 2012	*P. perforatus*	*R. ardua*	-1.20	-1.50	-2.06	-1.88	0.00	0.00	-1.14	-1.88	-1.08	-2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oct 2012	*P. perforatus*	*R. ardua*	0.29	0.40	0.00	0.00	0.00	0.00	0.56	0.56	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

May 2012	*P. perforatus*	*S. quintus*	-1.17	-2.13	-1.02	-1.64	0.53	0.39	-1.03	-2.10	-1.39	-3.00	0.25	0.27	0.00	0.00	0.00	0.00	-1.04	-0.62
Oct 2012	*P. perforatus*	*S. quintus*	1.64	1.11	0.00	0.00	0.96	0.92	1.18	0.89	0.00	0.00	0.25	0.37	0.00	0.00	0.00	0.00	0.00	0.00
May 2012	*P. capucinus*	*P. spinosa*	0.85	0.47	2.82	1.66	0.00	0.00	0.70	0.53	1.28	0.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oct 2012	*P. capucinus*	*P. spinosa*	0.97	2.17	1.64	2.88	0.23	0.14	0.58	1.27	1.36	1.64	0.00	0.00	0.06	1.76	-0.53	1.25	0.73	0.55
May 2012	*P. capucinus*	*P. phaenotus*	0.12	0.66	0.69	0.24	-0.75	0.38	0.07	0.59	1.92	0.41	-0.80	0.59	0.00	0.00	0.00	0.00	0.00	0.00
Oct 2012	*P. capucinus*	*P. phaenotus*	-0.81	1.45	-0.61	3.40	-0.62	-1.20	-0.63	1.02	0.00	1.29	0.00	0.00	-0.56	0.77	-0.25	1.53	0.00	0.00
May 2012	*P. capucinus*	*P. punctum*	2.48	2.30	2.30	2.93	-0.29	1.96	2.28	2.52	1.53	1.43	0.00	2.23	0.00	0.00	0.00	0.00	0.00	0.00
Oct 2012	*P. capucinus*	*P. punctum*	-1.28	2.28	-0.62	5.02	-1.04	-1.20	-1.40	1.40	-1.24	2.95	0.00	0.00	-0.42	1.59	0.00	2.48	0.00	0.00
May 2012	*P. capucinus*	*S. sculptus*	0.07	0.45	-1.39	-0.59	0.76	0.54	0.18	0.11	-1.29	-0.74	2.19	1.06	0.00	0.00	0.00	0.00	0.00	0.00
Oct 2012	*P. capucinus*	*S. sculptus*	-1.41	1.02	-1.30	0.82	0.00	0.00	-0.85	1.04	-0.32	1.68	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
May 2012	*P. capucinus*	*S. laevigatus*	-0.38	-0.64	0.59	-0.93	-1.10	0.42	-0.42	-0.63	1.87	-0.79	-1.14	0.57	0.00	0.00	0.00	0.00	0.00	0.00
Oct 2012	*P. capucinus*	*S. laevigatus*	-1.21	2.42	-0.52	4.09	0.00	0.00	-1.50	2.78	0.00	4.00	0.00	0.00	1.22	0.95	0.96	0.78	0.00	0.00
May 2012	*P. capucinus*	*S. quintus*	-0.66	1.39	0.04	2.07	0.76	0.42	-0.78	1.12	-0.74	1.11	0.58	0.40	0.00	0.00	0.00	0.00	0.00	0.00
Oct 2012	*P. capucinus*	*S. quintus*	1.05	2.55	0.41	2.96	0.94	0.69	0.15	2.21	0.28	2.16	0.00	0.00	1.06	2.18	-0.72	1.39	0.00	0.00
May 2012	*P. capucinus*	*T. incisellus*	0.00	0.94	2.11	1.33	-0.71	0.52	0.06	1.11	0.00	0.00	-0.66	0.86	0.00	0.00	0.00	0.00	0.00	0.00
Oct 2012	*P. capucinus*	*T. incisellus*	-0.15	2.39	0.40	2.82	0.33	0.29	-0.56	1.85	-0.27	2.29	0.00	0.00	1.49	1.29	1.20	0.75	0.00	0.00
May 2012	*P. capucinus*	*T. vel. sarekensis*	-0.70	1.02	-0.95	1.02	-0.68	-0.01	-0.62	1.19	-0.80	0.86	-0.40	0.33	0.00	0.00	0.00	0.00	0.00	0.00
Oct 2012	*P. capucinus*	*T. vel. sarekensis*	0.09	2.02	1.21	3.02	-1.69	0.50	0.19	1.66	1.16	2.39	0.00	0.00	0.23	1.69	1.22	0.94	0.00	0.00
May 2012	*P. nervosa*	*P. phaenotus*	-1.46	-2.18	-1.72	-2.14	-0.44	-0.89	-1.87	-1.88	-1.11	-2.03	-0.65	-0.70	-0.88	0.06	-1.43	-0.67	-0.59	-0.94
Oct 2012	*P. nervosa*	*P. phaenotus*	0.93	-1.15	-1.36	-1.56	1.96	0.22	0.81	-1.47	0.00	-1.82	1.43	0.48	0.10	-0.92	-1.42	-1.16	0.00	0.00
May 2012	*P. nervosa*	*P. punctum*	-0.04	1.50	-0.64	1.37	-0.10	-0.80	0.17	1.68	-0.71	2.16	0.00	-0.78	-0.61	-0.34	-0.70	-0.20	0.00	0.00
Oct 2012	*P. nervosa*	*P. punctum*	-0.74	-1.50	-0.66	-2.05	-0.52	-0.27	-0.57	-1.44	-0.85	-1.37	0.96	0.50	0.93	-0.22	0.00	-1.33	-0.56	-0.83
May 2012	*P. nervosa*	*R. ardua*	-1.89	0.98	-1.40	1.62	0.00	0.00	-1.85	1.11	-1.34	1.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oct 2012	*P. nervosa*	*R. ardua*	1.17	0.79	1.13	0.00	0.00	0.00	0.88	0.14	2.29	0.52	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
May 2012	*P. nervosa*	*S. sculptus*	0.93	1.02	-0.95	1.20	0.65	0.37	0.81	1.12	-0.35	0.70	0.92	0.65	-1.88	0.50	-1.15	0.64	0.00	0.00
Oct 2012	*P. nervosa*	*S. sculptus*	0.58	2.06	0.45	1.33	0.00	0.00	0.13	1.49	0.90	1.71	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
May 2012	*P. nervosa*	*S. laevigatus*	-2.01	-1.53	-0.56	-0.60	-1.33	-2.21	-2.11	-1.55	-1.12	-0.64	-2.06	-2.13	-0.27	-0.43	-0.16	-0.52	0.00	0.00
Oct 2012	*P. nervosa*	*S. laevigatus*	-0.52	-0.64	-0.21	-0.31	0.00	0.00	-1.23	-1.98	0.00	-1.48	0.00	0.00	0.59	0.20	-0.24	-0.01	0.00	0.00
May 2012	*P. nervosa*	*S. quintus*	-2.44	-0.57	-1.25	0.51	-2.59	-3.18	-2.09	-0.76	-1.63	0.86	-3.96	-4.90	-0.05	-0.09	-0.13	0.10	0.00	0.00

Oct 2012	*P. nervosa*	*S. quintus*	-1.54	-2.11	-0.35	0.24	-2.10	-2.52	-0.47	-1.45	0.79	-0.77	-1.60	-2.21	-1.48	-0.79	-0.94	1.18	1.07	0.92
May 2012	*P. nervosa*	*S. sarekensis*	0.00	0.00	-0.91	-2.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-1.41	-2.01	-1.06	-1.49	0.00	0.00
Oct 2012	*P. nervosa*	*S. sarekensis*	-0.72	-1.16	-0.90	-0.51	-0.92	-1.27	0.83	1.41	-0.37	0.92	0.56	0.39	-1.13	-1.33	-1.01	-1.11	0.00	0.00
May 2012	*P. nervosa*	*T. incisellus*	1.14	0.87	0.13	1.68	0.55	0.39	1.16	0.72	0.00	0.00	0.85	0.58	-0.35	1.91	0.04	2.54	0.00	0.00
Oct 2012	*P. nervosa*	*T. incisellus*	1.72	0.54	0.65	0.47	1.73	1.28	0.02	-0.51	0.38	-0.67	0.50	0.37	2.65	1.99	0.98	0.67	-0.29	0.86
May 2012	*P. nervosa*	*T. vel. sarekensis*	-0.22	1.26	0.44	1.65	-0.45	-0.96	-0.20	1.50	-0.35	1.62	-0.39	-0.77	2.57	1.75	0.74	0.53	0.00	0.00
Oct 2012	*P. nervosa*	*T. vel. sarekensis*	2.07	1.01	3.07	2.38	-0.36	0.00	-0.20	-1.28	1.48	-0.85	-1.06	-1.38	2.91	4.97	2.66	3.26	-1.66	-0.93
May 2012	*P. spinosa*	*P. phaenotus*	-0.64	1.60	0.71	0.60	0.00	0.00	-0.65	1.02	-0.44	1.30	0.00	0.00	2.55	1.02	0.25	0.07	0.00	0.00
Oct 2012	*P. spinosa*	*P. phaenotus*	-0.13	-1.60	1.04	-1.11	-0.52	-1.00	-0.37	-1.19	0.00	-1.26	0.00	0.00	-0.47	-1.12	0.69	-0.76	0.00	0.00
May 2012	*P. spinosa*	*P. punctum*	-0.44	-1.13	-1.60	-2.37	0.00	0.00	-0.37	-1.13	-0.77	-1.18	0.00	0.00	-0.66	-1.73	-1.36	-1.43	-0.44	-0.90
Oct 2012	*P. spinosa*	*P. punctum*	-1.79	-1.92	-1.25	-2.11	-0.94	-1.08	-0.94	-0.87	-0.60	-0.63	0.00	0.00	-0.87	-1.52	0.00	-1.13	0.00	0.00
May 2012	*P. spinosa*	*R. ardua*	-2.38	-2.38	0.89	0.14	0.00	0.00	-1.73	-2.29	-1.22	-2.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oct 2012	*P. spinosa*	*R. ardua*	-0.04	-0.30	0.31	0.00	0.00	0.00	-0.61	-1.18	-0.32	-0.68	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
May 2012	*P. spinosa*	*S. laevigatus*	-0.73	0.67	1.67	1.09	0.00	0.00	-0.85	0.75	-0.42	0.80	0.00	0.00	0.46	-0.12	0.61	0.18	1.88	2.27
Oct 2012	*P. spinosa*	*S. laevigatus*	-1.16	-1.82	0.32	-0.44	0.00	0.00	-0.94	-1.92	0.00	-1.46	0.00	0.00	-1.37	-1.83	-1.27	-1.25	-1.46	-1.62
May 2012	*P. spinosa*	*T. incisellus*	0.44	0.00	-1.61	0.30	0.00	0.00	0.24	0.23	0.00	0.00	0.00	0.00	-1.05	1.09	-0.58	1.89	1.83	1.22
Oct 2012	*P. spinosa*	*T. incisellus*	-1.70	-2.50	-0.51	-0.72	-3.39	-3.64	-1.32	-2.17	-1.30	-2.19	0.00	0.00	-0.72	-1.23	0.92	0.27	0.00	0.00
May 2012	*P. spinosa*	*T. vel. sarekensis*	-0.56	0.78	2.55	2.20	0.00	0.00	-0.55	0.78	-0.58	0.55	0.00	0.00	4.28	3.67	3.95	2.43	0.00	0.00
Oct 2012	*P. spinosa*	*T. vel. sarekensis*	0.16	-0.82	0.37	-0.38	0.73	0.40	-1.23	-1.98	-0.94	-1.50	0.00	0.00	0.99	0.14	0.87	-0.30	0.34	0.87
May 2012	*P. phaenotus*	*P. punctum*	0.43	0.25	-0.54	1.47	0.73	-1.46	0.47	0.20	-0.75	0.72	0.00	0.02	-0.38	-0.74	-0.96	1.08	0.90	0.16
Oct 2012	*P. phaenotus*	*P. punctum*	0.37	-1.57	0.37	-1.95	1.05	1.17	-0.42	-1.74	0.00	-2.08	0.32	1.55	0.90	-1.07	0.00	-1.24	0.00	0.00
May 2012	*P. phaenotus*	*S. laevigatus*	-1.67	-0.25	-0.65	-1.41	0.17	2.01	-1.47	-0.22	-1.16	-1.02	-0.81	0.58	1.76	1.26	-0.09	-0.67	0.00	0.00
Oct 2012	*P. phaenotus*	*S. laevigatus*	-0.60	-1.58	0.78	-1.32	0.00	0.00	-1.52	-2.52	0.00	-2.25	0.00	0.00	0.70	-0.07	1.46	0.34	1.94	-0.23
May 2012	*P. punctum*	*S. sculptus*	-1.17	-2.48	-0.79	-0.14	-0.33	-1.52	-1.37	-2.40	-1.35	-1.95	0.00	-1.43	-0.14	1.73	-0.33	2.29	0.00	0.00
Oct 2012	*P. punctum*	*S. sculptus*	-0.81	-0.26	-0.50	-0.62	0.00	0.00	-1.05	-1.05	-0.66	-0.71	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
May 2012	*P. punctum*	*S. laevigatus*	0.15	-0.35	-0.94	-0.61	2.84	0.05	0.15	-0.22	-1.53	-1.12	0.00	0.67	0.68	-1.18	-0.90	-1.27	0.00	0.00
Oct 2012	*P. punctum*	*S. laevigatus*	-0.82	-1.27	1.21	-0.59	0.00	0.00	-1.73	-2.29	0.00	-1.71	0.00	0.00	-0.56	-0.84	0.00	-0.68	0.00	0.00
May 2012	*P. punctum*	*T. vel. alatus*	2.21	0.85	2.29	1.33	0.00	0.00	1.88	0.92	1.36	0.78	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oct 2012	*P. punctum*	*T. vel. alatus*	-0.50	-0.80	-0.27	0.00	0.00	0.00	-0.53	-1.36	-0.31	-0.96	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

May 2012	*P. punctum*	*T. incisellus*	-0.65	-2.04	-1.44	0.54	2.29	-0.80	-0.80	-1.93	0.00	0.00	0.00	-1.35	0.72	1.48	-0.65	1.65	0.00	0.00
Oct 2012	*P. punctum*	*T. incisellus*	-1.11	-1.86	-1.14	-1.52	-0.02	-0.35	-1.19	-1.65	-1.19	-1.44	0.44	0.25	-0.67	-1.11	0.00	-0.92	0.00	0.00
May 2012	*P. punctum*	*T. vel. sarekensis*	0.15	-2.52	1.95	-0.85	-1.02	-2.46	0.18	-2.57	0.12	-1.80	0.00	-1.61	0.08	-0.86	1.49	0.56	0.00	0.00
Oct 2012	*P. punctum*	*T. vel. sarekensis*	-1.29	0.03	-0.14	-0.34	-1.67	2.05	-1.26	-1.56	-0.64	-1.41	-1.46	0.53	-0.95	2.13	0.00	0.13	0.00	0.00
May 2012	*R. ardua*	*S. quintus*	-1.32	-2.17	-0.34	-0.63	0.00	0.00	-1.18	-2.05	-0.99	-1.98	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oct 2012	*R. ardua*	*S. quintus*	-0.99	0.35	-1.28	0.00	0.00	0.00	-1.35	-0.59	-1.25	-0.36	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
May 2012	*S. laevigatus*	*S. quintus*	-1.87	-2.22	-0.49	-0.47	0.06	-0.72	-1.72	-2.17	-0.83	-1.58	-1.78	-2.71	0.73	0.65	-0.60	0.14	0.00	0.00
Oct 2012	*S. laevigatus*	*S. quintus*	2.02	0.78	1.64	2.80	0.00	0.00	-0.72	-1.44	0.00	-1.27	0.00	0.00	1.37	2.51	0.61	2.92	2.13	0.54
May 2012	*S. laevigatus*	*T. incisellus*	2.11	1.38	0.58	1.55	0.24	1.06	1.91	1.64	0.00	0.00	1.14	0.84	-0.79	1.31	-0.53	1.19	-0.93	-0.54
Oct 2012	*S. laevigatus*	*T. incisellus*	-0.73	-1.89	0.32	-0.04	0.00	0.00	-0.98	-2.21	0.00	-2.12	0.00	0.00	-0.36	-0.70	-0.05	0.30	0.00	0.00
May 2012	*S. laevigatus*	*T. vel. sarekensis*	-0.44	-1.04	-0.55	-2.02	1.57	-0.31	-0.32	-1.05	-0.67	-2.07	-0.48	-0.89	2.20	0.48	-0.10	-0.76	0.77	0.50
Oct 2012	*S. laevigatus*	*T. vel. sarekensis*	-0.12	0.00	-0.41	-0.43	0.00	0.00	-1.32	-2.08	0.00	-1.47	0.00	0.00	-0.02	-0.17	0.07	-0.69	-0.87	-0.46
May 2012	*S. sculptus*	*T. vel. sarekensis*	-1.48	-3.17	-0.24	-1.44	-0.90	-1.82	-1.36	-2.46	-0.83	-2.18	-0.85	-1.38	1.46	0.94	1.00	0.69	-1.39	0.48
Oct 2012	*S. sculptus*	*T. vel. sarekensis*	-0.31	0.35	0.00	0.94	0.00	0.00	-0.06	0.26	0.64	0.32	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
May 2012	*S. quintus*	*T. incisellus*	1.17	0.73	0.15	2.33	-0.07	-0.67	1.06	0.56	0.00	0.00	0.75	0.58	0.40	1.80	0.69	3.14	0.72	0.44
Oct 2012	*S. quintus*	*T. incisellus*	0.10	-1.23	-0.65	0.37	-0.24	-0.80	-1.32	-2.04	-1.36	-2.01	0.25	0.23	1.99	0.94	1.83	1.58	0.00	0.00
May 2012	*S. quintus*	*T. vel. sarekensis*	0.09	-1.47	0.37	-0.08	-1.01	-0.85	0.10	-1.53	0.18	-1.37	-0.27	-0.87	-0.01	1.07	-0.10	0.96	1.00	-0.53
Oct 2012	*S. quintus*	*T. vel. sarekensis*	-0.94	-0.04	-0.53	1.58	-0.85	-0.72	-1.60	-2.41	-1.00	-1.40	-2.06	-2.59	1.06	3.26	-0.03	3.08	0.00	0.00
May 2012	*S. sarekensis*	*T. incisellus*	0.00	0.00	1.31	1.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.11	1.89	2.82	1.82	0.00	0.00
Oct 2012	*S. sarekensis*	*T. incisellus*	1.11	-0.08	0.10	-0.80	0.81	0.62	-0.03	-0.93	-0.82	-1.83	0.20	0.27	1.62	0.90	0.92	0.15	1.80	1.11
May 2012	*T. incisellus*	*T. vel. sarekensis*	0.35	-0.91	2.13	0.76	2.00	-0.31	0.72	-0.99	0.00	0.00	1.73	-0.20	3.05	1.31	1.37	0.83	0.00	0.00
Oct 2012	*T. incisellus*	*T. vel. sarekensis*	0.73	-0.77	0.21	0.13	0.98	0.65	-0.39	-1.32	-0.45	-1.63	0.47	0.27	1.13	0.34	0.76	-0.08	0.00	0.00

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