

**„Arthropod food-webs on man-made lake islands.“**

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*„No man is an island“*

John Donne, 1624

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## **Appendix A**

*Species/Site matrices of ground beetles and spiders caught in June 2010*

## **Appendix B**

*Biplots of  $\delta^{13}C$  and  $\delta^{15}N$  for all species analyzed on e*

## Abstract

Food webs are the dynamic structure of natural ecosystems. Island biogeographical and meta-community perspectives have aided food web research in spatially delimiting and opening the the studied object at the same time. While islands and habitat fragments have become empirical representations of spatially delimited focal habitat patches and their dynamics, considering the dispersal of organisms between them has opened new perspectives on community assembly and the maintenance of biodiversity. Furthermore, the spillover of organisms between adjacent habitats has been integrated into studying the dynamics of local ecosystem processes. These 'spatial subsidies' can generate strong interdependencies between the food webs of adjoined habitats, as different as terrestrial and aquatic ones. When studying the effects of ecosystem size and spatial subsidies on community and food web properties, islands have a prominent role in testing appropriate ecological hypotheses. In this study, the effect of ecosystem size in determining the food chain length of arthropod communities was investigated on young man-made lake islands of restored lakes in the Lower Rhine area. Moreover, it was analyzed how the importance of spatial subsidies for local food webs varied with island area and which role dispersal and adaptations to local conditions have in determining the community composition of large and small islands. Food chain length and spatial subsidies were tracked with a stable isotope approach. A strong relationship between food chain length and island area could be shown, while the importance of spatial subsidies, which was restricted to a few species, decreased with island size. It could be shown, that the species richness of spiders and ground beetles tracked an increasing spatial heterogeneity with increasing island size and arthropods were significantly assorted to spatially varying environmental conditions.

# Zusammenfassung

Nahrungsnetze sind die dynamische Struktur natürlicher Ökosysteme. Aus dem Blickwinkel der Insel-Biogeographie und der Meta-Community-Theorie wurden Nahrungsnetze räumlich abgegrenzt und geöffnet zugleich. Während Inseln zu den Repräsentationen jener räumlich abgegrenzten, fokalen Habitats wurden, welche die Ökologie bis dahin studiert hatte, öffnete die Berücksichtigung der Artenverbreitung zwischen den Habitats neue Perspektiven auf den Entstehungsprozess natürlicher Artengemeinschaften und den Erhalt der Biodiversität. Auch die Überlappung der Aktivität vieler Arten zwischen angrenzenden Ökosystemen wurde in die Untersuchungen lokaler Habitats integriert. Diese ‚spatial subsidies‘ können starke wechselseitige Abhängigkeiten zwischen Nahrungsnetzen erzeugen, die so verschieden sind wie jene aquatischer und terrestrischer Systeme. Inseln spielen eine herausragende Rolle in der Erforschung der Einflüsse von Ökosystemgröße und ‚spatial subsidies‘ auf Artengemeinschaften und deren Nahrungsnetze. In dieser Studie wird der Effekt der Ökosystemgröße auf die Nahrungskettenlänge in Arthropodengemeinschaften auf jungen, künstlich aufgeschütteten Inseln in Süßwasserseen am Niederrhein untersucht. Darüber hinaus wurde untersucht, wie der Anteil von ‚spatial subsidies‘ an Nahrungsnetzen mit der Inselgröße variiert und welchen Einfluss Verbreitung und Anpassung an lokale Bedingungen auf die Zusammensetzung von Artengemeinschaften auf kleinen und großen Inseln haben. Nahrungskettenlänge und ‚spatial subsidies‘ wurden anhand stabiler Isotopen untersucht. Ein starker Zusammenhang zwischen Inselgröße und Nahrungskettenlänge konnte nachgewiesen werden. Auch der Einfluss von ‚spatial subsidies‘, welcher auf wenige Arten begrenzt war, nahm mit der Inselgröße ab. Es konnte gezeigt werden, dass die mit der Inselgröße zunehmende Habitatdiversität die Artenvielfalt von Laufkäfern und Spinnen bestimmte und diese sich anhand variierender Umweltbedingungen räumlich verteilten.

## Introduction

Ecologists study the principles of nature from a systems perspective, emphasizing the interdependence of organisms, related to each other and their environment by direct and indirect interactions. The term “ecosystem” was first coined by Sir Arthur Tansley as a refutation of holistic views of the world, which perceived nature as an organism (Clements 1916; Tansley 1935). Both concepts have approved that organisms are linked to their environments via the adaptation to abiotic conditions, which consequently were identified as a major cause for the distribution of different biota. Thus, the interacting elements of a natural system - the organisms present - are co-determined by a set of physicochemical preconditions, which in turn are subjected to spatiotemporal variation. However, the dynamics of a system are predominantly constituted by the interactions of the organisms themselves. A system can be defined as the following: “a group of devices or artificial objects or an organization forming a network especially for distributing something or serving a common purpose [...]” (*Merriam-Webster Online Dictionary copyright © 2012 by Merriam-Webster, Incorporated*). In this definition, the components or elements of a given system interact by transmitting something between them. In natural systems, the majority of interactions are related to the transfer of nutrients and energy. The complex networks of interactions in these natural systems, dealing with the distribution of energy and nutrients, have been termed ‘food webs’ (Elton 1927; Garlaschelli *et al.* 2003). Indeed most other interactions between the organisms within ecosystems are related to some kind of food-web interaction. Exploitative competition (Wootton 1994), mutualistic interactions as between ants and plants (Heil & McKey 2003), seed dispersal by animals (Howe & Smallwood 1982), cleaning mutualisms (Cheney & Côté 2005), pollination of plants by insects, birds and bats (Fleming & Muchhala 2008) or sometimes simply the supply of structural components for the foraging of predators, as the dense branching of woody plants that aids net-building spiders (Colebourn 1974; Uetz 1991): All these interactions emerged in ecology and evolution subsequent to the acquisition of nutrients of energy. Thus, the ‘trophic dynamic aspect in ecology’ is the fundamental force of integration within every ecosystem (Lindeman 1942). Describing the flux of nutrients and energy through ecosystems has been an important cornerstone of ecology and identifying major components and quantifying transmission rates between them has shaped the public perception and education of ecological sciences (Odum & Odum 1955; Odum 1957). Another approach within ecology is to examine food webs and food web dynamics as ecological units of their own, excluding abiotic components or parameters, which are otherwise included into the ecosystem concept. Food web research primarily focuses on the complex network of trophic interactions between interdependent species and how structural properties of these networks vary with some factor (Briand 1983; Briand & Cohen 1987; Petchey *et al.* 1999). Early simulations of complex food web networks suggested that the stability of a food web decreases with increasing complexity, but that food webs were more stable, when they were divided into compartments (May 1973; Pimm & Lawton 1980). In such compartments, species interact significantly more often with each other than with species outside of these compartments. Later studies demonstrated that even the most simple food webs exhibit chaotic behavior (Hastings & Powell 1991; Becks *et al.* 2005; Benincà *et al.* 2008). However, the “complexity-stability debate” is still ongoing and recently the number of studies that reveal mechanisms that enhance the stability of complex food webs has increased (Dunne *et al.* 2002; Brose *et al.* 2006; Neutel *et al.* 2007). Additionally, recent studies have confirmed the compartmentalization of real natural food webs (Raffaelli & Hall 1992; Krause *et al.* 2003; Rezende *et al.* 2009) and that the subdivision of food webs into compartments indeed enhances stability (Rooney *et al.* 2006; Thébault & Fontaine 2010; Stouffer & Bascompte). Other subdivisions of food webs were introduced to ease their understanding or to reduce complexity for statistical analysis. In classical food webs, species in overlapping predator-prey interactions were often lumped to ‘trophic species’ (Cohen & Briand 1984;



Solow & Beet 1998), since the density of trophic links were assumed to be scale invariant, i.e. food webs properties were assumed to change little if at all with the resolution of taxonomic data (Briand & Cohen 1984; Sugihara *et al.* 1989). This assumption was disproved in empirical studies later (Martinez 1992, 1994), underlining that taxonomic resolution and study scale are important in food web research and artificial reductions lead to inconsistent results.

Furthermore, it was noted that the interactions between species were not equivalent. Predators prey on some prey species more frequent than on other prey species. This variation in the frequency of trophic interactions between species pairs has been termed ‘interaction strength’ and it depends on the abundance of consumer and prey, food preferences of the consumer and other factors that limit the prey process (Paine 1980; Wootton & Emmerson 2005). An example of weak interactions is the low prey specificity of generalist species. In contrast, a specialist predator imposes strong influence on the population dynamics of its preferred prey. This recognition of unequal energy flows in different predator-prey interactions has led to the distinction of ‘connectance webs’, which do not integrate interaction strength and ‘energy webs’, which include interaction strength into all measures of the web (Post 2002b). Interaction strength is typically measured by experimental species removal and subsequent shifts in community composition or population density of an assumed prey species (Paine 1992; Laska & Wootton 1998). It has been found that certain patterns of interaction strength can have stabilizing effects on food webs (de Ruiter *et al.* 1995; Emmerson & Raffaelli 2004) and more recent studies emphasize the importance of the numerous weak interactions within food webs (McCann *et al.* 1998; Berlow 1999; Neutel *et al.* 2002). It was also assumed that some sequences of linkage are very rare. One of these linkages is a loop chain. If species A feed on species B, which feeds on species C, species C is closing a ‘loop’, if it feeds on species A. The assumed rarity of such loops was based on constraints of energy flow between species and on size preferences, i.e. large predators eat smaller prey, which makes food web loops unlikely.

The most widespread and accepted subdivision of food webs is that into trophic levels. Species within food webs are assigned to trophic levels, in which all species feed on other species aggregated in the trophic level below, which is closer to the abiotic nutrients. The lowest trophic level contains the primary producers like vascular plants, aquatic algae and autotrophic bacteria, which convert inorganic compounds and an abiotic source of energy - in most cases light - into organic biomass. The second trophic level is constituted by primary consumers, herbivores and grazers, which feed on primary producers. Secondary consumers, predators that feed on primary consumers, constitute the third trophic level. If this secondary consumer is not preyed upon by another species, it is called the “top predator”, but often parasites and hyper-parasites that acquire their energy and nutrients through the consumption of animal predator tissues constitute additional trophic levels. Energy and nutrients of all trophic levels are furthermore routed to the detrital food web with the gradual dissipation of energy and the cycling of nutrients through re-mineralization. The gradual dissipation of energy, i.e. the inefficiency of the energy transfer between trophic levels has led to the assumption that the number of trophic levels in food webs is limited (Kozlovsky 1968). Furthermore, predators are almost always less abundant than their prey and their populations are thus more prone to stochastic extinctions and disturbance, potentially limiting the occurrence of higher trophic levels (Pimm & Lawton 1977). Indeed, in the trophic pyramid, the biomass of higher trophic levels is only a fraction of the basal production (Lindeman 1942). Classical food webs have suggested that food chains of terrestrial systems are shorter than aquatic food chains, but it is still an ongoing debate, if these differences are real (Chase 2000; Shurin *et al.* 2006). Differences in food chain length are thought to have drastic consequences for the biomass distribution between different trophic levels. In a process called ‘trophic cascade’, a secondary consumer, which controls an herbivore population will in turn facilitate the population of the primary producers. So, in food chains with even numbers the primary producers are

assumed to be “top-down-controlled” by their herbivores, while in food chains with odd numbers, primary producers were assumed to be “bottom-up-controlled” by the availability of nutrients (Fretwell 1977; Oksanen *et al.* 1981). The theory of this dynamics originated in the long standing question in ecology, “why parts of the world are green” (Hairston *et al.* 1960). Stated in another, more extreme way, the question was “Why have herbivores not driven plants to extinction?” In the framework of ‘trophic cascades’ it was of course assumed that herbivores are controlled by their predators, an assumption made by the original “Green World Hypothesis” by Hairston *et al.* (1960). Other authors have stated that primary production by plants is mostly climate and soil nutrient controlled and herbivore control of primary producers is spatially restricted to local phenomena (Polis 1999). Herbivory in terrestrial systems was found to remove less than 10 % of the primary production in most cases, although ungulate grazers can remove 90 % in some habitats. However, in aquatic systems, microalgae are completely removed in many habitats, while patterns of herbivory on aquatic macrophytes are similar to those of terrestrial plants (Cyr & Pace 1993). The search for mechanisms of these findings is deeply intertwined with the finding that trophic cascades are actually found in natural communities (Pace *et al.* 1999; Schmitz *et al.* 2000) and are much stronger in freshwater systems than in marine and terrestrial ecosystems (Shurin *et al.* 2002).

Some studies deny the concept of discrete trophic levels altogether with strong arguments and empirical data (Polis 1991; Polis & Strong 1996). Already in 1961 R.M. Darnell observed difficulties in assigning species to discrete trophic levels and proposed the term ‘trophic spectrum’ (Darnell 1961; Paine 1980). Gary Polis (1991) investigated desert food webs and found a high proportion of omnivory and feeding loops, unprecedented in the literature, which emerged due to ontogenetic diet shifts in the life history of most animals. Adult animals feed on different prey than their smaller progeny or their larval stages. This leads to the fact that predatory species downright “eat each other”, when an adult individual of one predacious species feeds on the progeny of another predacious species and vice versa (Polis 1988). If this, usually size dependent phenomenon occurs within species populations, it is called cannibalism (Fox 1975). If it occurs between different predator species, it is called intra-guild predation (Polis *et al.* 1989). Strictly interpreted, intra-guild predation (IGP) is difficult to separate from omnivory insofar as in IGP a predator does indeed feed on more than one trophic level, the way omnivory was defined by Pimm and Lawton (1978). However, most authors use the term omnivory for predators feeding at the plant-herbivore interface, while intra-guild predation is used for trophic interactions between potential competitors at the top of the food-web (Polis & Holt 1992; Coll & Guershon 2002). All of these concepts that potentially complicate food webs were found to be widespread in nature (Neutel *et al.* 2002; Arim & Marquet 2004; Gagnon *et al.* 2011) and it has been widely accepted that they somewhat blur the concept of trophic levels. Nonetheless, there have been also strong advocates for the concept of trophic levels, which argue that trophic levels are real at least for plants and obligate herbivores and that the existence of trophic cascades found in diverse ecosystems proves the existence of trophic levels (Hairston & Hairston 1997; Williams & Martinez 2004). Post and Takimoto even proposed IGP as one of three proximate mechanisms for a variation in food-chain length (Post & Takimoto 2007; Takimoto *et al.* 2008). Polis *et al.* (2000) in turn have argued that most studies confirming the existence of trophic cascades in terrestrial food webs, have really proven the existence of trophic cascades at the species level within food chains that were only a subset of the investigated community. Furthermore the authors stated that community wide trophic cascades have been rarely observed in ecological studies. Up to date, it seems that both aspects are real in natural ecosystems. Discrete trophic levels are easily resolved for plants and herbivores (level 0 - 1), but higher levels (> 1) are more and more blurred and their linking patterns are not distinguishable from randomly generated food webs (Thompson *et al.* 2007), but sometimes contradictory results are found (Thompson *et al.* 2009). Sometimes, the question whether a top trophic level exists or not, depends on the uncertain spatial distribution and foraging range of top predators. Finally, the search

for an answer to the question, how prevalent omnivory or discrete trophic levels are in natural systems, is also hampered by methodological difficulties. The desire to make models of food web structure accessible to comparative analysis has made researchers readily accept the convenient idea of food web structures as ecological still lifes, similar to their graphic representations. Thus, the majority of food-web records in literature are reported as either “cumulative” or “time specific”, i.e. without temporal or spatial resolution (Schoenly & Cohen 1991; Ings *et al.* 2009). Cumulative food webs summarize trophic interactions from observations at different points in time and space in static network-images or interaction matrices. This compositional augmentation of trophic interaction links is remarkable, because real food webs solely exist as “possible interaction networks of species overlapping in their phenology” and thus merely as a fraction of the corresponding cumulative food web at a given time. As a result, cumulative food webs tend to overestimate the density of trophic links and underestimate the percentage of basal species such as plants relative to “time-specific webs” (Pimm *et al.* 1991; Schoenly & Cohen 1991). A significant part of food web research therefore depends much on details, which are very hard to be gathered as data. The complexity of food web links and interactions has been described for desert systems, which were assumed to be very simple in structure. 100 prey species were observed for a single scorpion species in 181 survey nights and a yield effort curve suggested that the true number of prey species was much higher (Polis 1991).

Despite these uncertainties, the research on the dynamics and limitations of food-chains is continued and it has become indisputable that at least the local extinction of strong inter-actors at the top of dominant food chains imposes severe consequences at the ecosystem level in biomes all over the world (Estes *et al.* 2011). Consequently, ecological sciences have paid particular attention to the factors that limit the number of trophic levels or food-chain length, respectively. According to the hypothesis of Pimm and Lawton (1977) higher trophic levels are more prone to stochastic population dynamics, since abundances decrease with the trophic level and thus they also should be more prone to disturbances and be less resilient, i.e. they are more inertial in their return to the initial state before the disturbance event. Although there is some evidence for an influence of disturbance on food-chain length (Jenkins *et al.* 1992; McHugh *et al.* 2010) most studies did not find any relationship (Sterner *et al.* 1997; Takimoto *et al.* 2008; Walters & Post 2008).

It was also hypothesized that food-chain length is limited by primary productivity, so that nutrient poor ecosystems should have shorter food-chains. It is intuitively clear that a higher availability of nutrients within an ecosystem and a consequently higher primary productivity would facilitate larger populations of herbivores, which in turn would feed larger populations of predators. Populations on higher trophic levels would thus be less prone to stochastic extinctions and longer food-chains would be feasible (Yodzis 1984). Despite this simple logic behind the hypothesis, initial studies to clarify the question found that food-chain length was independent of productivity (Briand & Cohen 1987) and the results of later studies varied, with some authors confirming the relationship of food-chain length and productivity (Carpenter *et al.* 1987; Persson *et al.* 1992; Young *et al.* 2013) and others that found no such relationship (Spencer & Warren 1996; Wootton *et al.* 1996). Plant defensive mechanisms and inedible plant parts like structural carbon components were considered to hamper a consumption of the total primary productivity by some authors and studies. They linked food-chain length to the proportion of primary productivity that is available to consumers (‘edible carbon’) and could indeed confirm a relationship (Kaunzinger & Morin 1998; Doi *et al.* 2009). An expansion of the ‘productivity hypothesis’ is the hypothesis of ‘productive space’, which explicitly adds a spatial component to the relationship (Schoener 1989). It has been doubted that the effects of per unit area productivity and space could be disentangled in field studies (Cohen & Newman 1991) and the productive space hypothesis was later rejected empirically (Vander Zanden *et al.* 1999; Post 2007). Thus, the low theoretical support for the impact of productivity on food-chain length in general points at a stronger

impact of ecosystem size alone (Post 2002a). The influence of ecosystem size on community wide food-chain length has been confirmed by several studies in aquatic systems (Vander Zanden *et al.* 1999; Post *et al.* 2000a; Thompson & Townsend 2005; Doi *et al.* 2009; McHugh *et al.* 2010). In terrestrial systems, community wide effects on food-chain length are poorly studied (Takimoto *et al.* 2008), but results from food-chains of ‘stacked specialists’ in forest and grassland fragments indicate that such a relationship could be also common in terrestrial systems (Komonen *et al.* 2000; Kruess & Tschardtke 2000).

The effects of spatial parameters on community properties like the species area relationship (SAR) are among the oldest and most recognized principles in ecology (Arrhenius 1921; Lawton 1999). An increase in the number of species with habitat area has been confirmed for a wide range of habitats and organisms (Lomolino & Weiser 2001). The underlying mechanisms of SARs are still debated and are likely not as general as the resulting pattern. The area *per se* hypothesis assumes that larger areas reduce the probability of stochastic species extinctions by supporting larger and greater numbers of populations (Preston 1960; MacArthur & Wilson 1963). SARs have been also explained by passive sampling (Connor & McCoy 1979; Lomolino 1990), neutral models (Bell 2001; Hubbell 2001) and multiple interacting causes (Shmida & Wilson 1985). Another strain of theory is based on the niche concept (Hutchinson 1959) and argues that environmental heterogeneity - the diversity of different environmental conditions - often increases with increasing habitat area, thereby providing an increasing amount of distinct niches for species adapted to them (Williams 1964). The influence of habitat heterogeneity on species-area relationships has been confirmed experimentally (Simberloff & Abele 1976; Douglas & Lake 1994), but most studies have tried to disentangle heterogeneity from area *per se* effects statistically. They found varying degrees of interaction between the two variables (Kohn & Walsh 1994; Triantis *et al.* 2005; Kallimanis *et al.* 2008) and sometimes the strength of the interaction varied between different groups of organisms (Ricklefs & Lovette 1999). Although there is an increasing awareness that the heterogeneity-area tradeoff is deeply rooted in niche properties and dynamics of individual populations and communities (Allouche *et al.* 2012), no study today has tried to relate the diversity of species niche properties to area directly. Instead, most studies examined the correlation of some measurement of habitat diversity and species diversity. This has various reasons, which are mostly interdependent, but the most common is that consistent data on niche properties and reliable information about which habitat factor is the most influential are rarely available for the whole species community in focus or in published datasets.

Considering ecosystem size as one of the most pervasive impacts on food-chain length, the question arises, how food-webs or ecosystems are delimited in the first place. Where do ecosystems start and other ones end and how are local food webs assembled? Since predators and their prey vary in mobility, top predators probably cannot be assigned to a particular local food web (Polis & Hurd 1996). Thus, dynamics between ecosystems and communities might be as important in structuring food webs, as local conditions and processes.

The spatial delimitation of ecosystems is anything else than straight forward and it has been repeatedly proposed to drop the ecosystem concept altogether, referring to the openness of natural systems as one of the strongest arguments (O'Neill 2001). Islands are commonly perceived as the spatially most delimited ecosystems on earth and thus they were considered to be excellent model systems to investigate the spatial dynamics of community assembly and variation of community properties with island size. The first to outline a theory of these processes on islands were Edward O. Wilson and Robert MacArthur in their “Theory of Island Biogeography” (IBT) (MacArthur & Wilson 1963; 1967). An identical theory was developed 10 years before by Eugene Munroe (1953), but was not recognized at the time (Brown & Lomolino 1989). The IBT states that the species richness on an island is a dynamic equilibrium between the immigration and extinction of species. When an island is

colonized by species from the mainland, at first species with a high dispersal capacity arrive. The number of new species arriving on an island decreases with time. With each species arriving on an island, the number of interactions between species on the island increases and subsequently the number of extinction events increases. Thus the species assemblage on an island is subject to a constant species turnover. The immigration and extinction curves were proposed to be concave, due to the non-linearity of the variable probabilities of immigration and extinction over time (Gilpin & Armstrong 1981). Island size and island isolation were the two factors that were considered to further affect the equilibrium. Immigration rates were considered to be most impacted by island isolation, while island extinction was thought to be most dependent on island size. Later, hypotheses were proposed and tested, which stated that immigration rates are also affected by island size in what was called 'target effect' or 'passive sampling effect' (Lomolino 1990). Furthermore, island isolation was proposed to affect extinction rates, since dispersing individuals from the mainland can complement decreasing populations on islands more likely, if islands are less isolated (Brown & Kodric-Brown 1977). This was called the 'rescue effect'. If immigration rates from a source pool with positive population growth of a species are high enough to override the decline of this species population in the recipient community on an island (a population sink), these processes are called source-sink dynamics (Holt 1985). The IBT was empirically tested in a great number of studies, (Reviewed in Losos & Ricklefs 2009). Initial studies could confirm the IBT on mangrove-islands that were completely defaunated with methyl-bromide. Species richness of arthropods on these island forming mangrove trees increased over time via colonization and subsequently decreased via local extinction of arthropod species again to reach a plateau, or equilibrium, respectively (Simberloff & Wilson 1969, 1970). Later, studies appeared which could show also non-equilibrium states of island species richness (Thornton *et al.* 1993; Morrison 2002). Although some studies argue, that the equilibrium theory of island biogeography is virtually refuted or at best locally limited and non-equilibrium models are more likely to be general (Heaney 2000; Whittaker 2000), it seems that no end to the question is yet in sight (Schoener 2009).

Island biogeographical patterns were not only studied on real islands but also in habitat fragments that were hypothesized to be similarly isolated as real oceanic islands. Moreover, IBT has initiated the still ongoing debate about whether natural reserves should consist of a single large area or several small areas, the so called SLOSS debate (Diamond 1975b) and has therefore markedly changed the face of conservation sciences. In turn, the theory of island biogeography was no longer restricted to terrestrial habitats surrounded by water (Krauss *et al.* 2003). Instead, water was substituted by a distinct habitat surrounding the focal patch, called the 'matrix' (Debinski & Holt 2000).

Spatial processes between geographically isolated habitat patches have been investigated also in theories of population ecology, which were developed concurrently to IBT. Populations in local habitat patches are connected to each other via dispersal, resulting in the interdependence of local population dynamics, regionally shaping what has been termed a 'metapopulation' (Hanski & Gilpin 1991). Classical effects of area and isolation on the dispersal and distribution of animals, established by the IBT, have been integrated into metapopulation dynamics to elucidate population patterns in terrestrial habitat fragments (Hanski 1998). Later, the concept of metapopulation dynamics has been extended to whole communities in meta-community dynamics (Leibold *et al.* 2004), accounting for the simple fact, that meta-population dynamics apply to the most of potentially interacting species within a community and thus also community dynamics are regionally linked by the dispersal of species. In IBT and meta-community theory, communities are affected by stochastic local events of extinction and by the immigration of species from outside the community. The major difference between classical island biogeography and theories of population and community dynamics on multiple scales is the direction of species dispersal and the definition of the species pool. In classical

IBT, the species pool is defined as a source community on a “continental mainland” from which species disperse to recipient communities on more or less isolated islands. In meta-population and meta-community dynamics all local habitat patches within a region, potentially connected via species dispersal, constitute the regional species pool.

Meta-community dynamics can be subdivided into four major perspectives, which emphasize different processes within regional meta-communities and do not mutually exclude each other. The ‘patch dynamic perspective’ focuses on the multi-directional dispersal of different species between homogenous local patches, often formulated as patch occupancy dynamics, in which local processes are supposed to shape local communities faster than dispersal processes between them. The perspective of ‘species sorting’ assumes the heterogeneity of one or several environmental factors between local habitat patches and builds on classical theories of niche separation and coexistence. Species are assumed to be sorted along environmental gradients, since local processes of competition and extinction, mediated by differences in species adaptations to local conditions, occur faster and have larger impact on local communities than dispersal processes between them. From a species sorting perspective, species are unable to locally persist in ‘sink habitats’. In contrast, if high dispersal rates between patches override local processes of competition and extinction and dominant species from very productive source communities are able to persist in source-sink dynamics, this is a so called ‘mass effect’. From a mass effects perspective, regional dispersal processes are also the key mechanism in the resilience of local patches after disturbance. Community composition will therefore be regenerated or renewed according to regional abundance distributions and dispersal capacities (Holyoak *et al.* 2005). All of the perspectives described above assume that species differ in their adaptation to environmental or biotic conditions. If these differences are neglected, meta-community dynamics can be viewed from a neutral perspective and species distributions are random auto-correlated assemblages in space and time (Hubbell 2001).

Ecosystems and their core dynamics within food webs are thus not solely affected by local processes. The structure of local food webs can be also governed by immigration processes, mass effects and patch dynamics on a more regional scale. If the population persistence of basal prey species or predators is influenced by dispersal between habitat patches, then meta-community dynamics can affect food web structure via bottom-up and top-down effects in trophic cascades, potentially determining food-chain length (Holt 2002; Holt & Hoopes 2005). Often, species in food webs are hierarchically organized into spatial domains according to their trophic level. Top predators might have a higher mobility and a larger foraging range than an intermediate predator or a basal prey species and therefore spatially integrate a number of smaller habitat patches (Rose & Polis 2000; Holt 2002). This can be partially seen as a spatially explicit model of size structured food webs, when organism size is directly related to foraging range. Additionally, the spatial dynamics of a single keystone predator may have profound community wide effects on multiple trophic levels of local food webs (Miller & Kneitel 2005). These spatial effects may structure communities and food webs even after a top or keystone predator has gone locally extinct (McCoy *et al.* 2009). The latter example illustrates, how important the integration of spatial processes within a wider meta-community context can be, when trying to investigate the determinants of local food web structure.

Island biogeography and meta-community dynamics both focus on the dispersal and distribution between geographically isolated, but ecologically similar ecosystems, but a growing number of studies and new emerging concepts illuminate the manifold interactions between adjacent, ecologically different ecosystems, or spoken in the language of spatial ecology: Interactions between the focal habitat patch and its surrounding matrix. These concepts consider the everyday reality of the cross boundary movement of organisms or materials between adjacent ecosystems and have been integrated into theories of landscape ecology (Polis *et al.* 2004) and meta-ecosystem dynamics (Loreau *et al.*

2003). The recognition of ecosystem openness has led to a number of studies that have doubted the spatial delimitation of habitat fragments and investigations that have shown how communities in these fragments are impacted by species migration and spill-over from the matrix (Ås 1993; Cook *et al.* 2002; Brotons *et al.* 2003).

Historically, studies in lentic and lotic freshwater ecosystems were the first to recognize the profound impacts of 'allochthonous intakes' and to integrate them in to concepts of ecosystem dynamics, although it was recognized early that fluxes of nutrients and organisms between aquatic and terrestrial ecosystems are reciprocal (Likens & Bormann 1974). The river continuum concept (Vannote *et al.* 1980) acknowledges the key role of the surrounding riparian vegetation in structuring communities and food web dynamics in small streams and rivers via the input of leaf litter, but also nutrient run-offs and intake of humic substances from terrestrial ecosystems directly impact river systems, in particular during seasonal high waters (Bayley 1995) and in rural catchments (Dodds 2006). But also marine coastal systems and coral reefs are affected by nutrient run offs via the transport of nutrients in river ecosystems to estuaries (Furnas 2003; Fabricius 2005). Inputs of terrestrial leaf litter also indirectly impact freshwater systems, since the increase of humic substances and DOC content can affect light attenuation and thereby primary productivity and trophic structure in the water column of freshwater lakes (Karlsson *et al.* 2009). Moreover, some unproductive lakes are shaped by the import of terrestrial carbon sources (Jansson *et al.* 2007), which account for between 50 % and 80 % of the carbon intake of fishes (Carpenter *et al.* 2005). Additionally, lake morphometry and depth determine the importance of allochthonous intakes or autochthonous productivity. But also allochthonous nutrient inputs from aquatic systems to terrestrial habitats have been documented and investigated. The most prominent examples are bird colonies on coastal strips and islands, where waterfowl deposit nutrients that origin in food-webs of the adjacent marine ecosystem via feces, feathers and carcasses (Stapp *et al.* 1999; Sanchez-Pinero & Polis 2000; Havik *et al.* 2014).

A great number of studies investigated the flux of organisms between adjacent ecosystems. In particular the emergence of aquatic insects and their subsidy to terrestrial food webs has been of interest. Aquatic insects can reach high local densities and their export to terrestrial systems can exceed local terrestrial secondary production adjacent to their aquatic habitats (Jackson & Fisher 1986; Bartrons *et al.* 2013). Although most studies investigated aquatic-terrestrial links between streams and riparian habitats, the export of emerging insects from lakes can exceed that from streams (Gratton & VanderZanden 2009). Fluxes of organisms across boundaries other than the aquatic-terrestrial interface have also been investigated and fluxes may ultimately depend on properties of the boundaries themselves (Wiens *et al.* 1985; Cadenasso *et al.* 2003; Witman *et al.* 2004). The flux of organisms across ecosystems can affect the abundance, biomass and trophic structure of consumers in the subsidized system via multiple pathways. While they can be consumed directly by terrestrial predators, their carcasses also subsidize the detrital food-web and facultative scavengers (Polis & Strong 1996; Dreyer *et al.* 2012). But also the subsidy of terrestrial herbivores via the deposition of aquatic algae has been demonstrated (Bastow *et al.* 2002). A plethora of studies has investigated the subsidy of aquatic insects to spiders in terrestrial ecosystems adjacent to streams, which was considered as the most common aquatic-terrestrial food web link with the highest impact (e.g. Williams *et al.* 1995; Henschel *et al.* 2001; Collier *et al.* 2002; Kato *et al.* 2003; Sanzone *et al.* 2003; Akamatsu *et al.* 2004; Kato *et al.* 2004; Briers *et al.* 2005; Paetzold *et al.* 2005; Akamatsu *et al.* 2007; Marczak & Richardson 2007). Furthermore, spiders have been identified as dominant consumers of aquatic prey also on lake shores (Jonsson & Wardle 2009; Hoekman *et al.* 2011) and in coastal ecosystems (Anderson & Polis 1998; Mellbrand *et al.* 2011) and on islands (Polis & Hurd 1995).

Meanwhile, the evidence for aquatic-terrestrial food web links has been strong enough for many researchers to take the next step and explore the dynamics and food-web impacts of cross-ecosystem

linkages. One of the earliest mechanisms, shown by studies of cross-ecosystem linkages was apparent competition between aquatic insects and terrestrial herbivores. Through the facilitation of riparian predator communities the predation rate on terrestrial herbivores increased and subsequently, herbivore abundance was reduced in areas where emergence of aquatic insects was high (Henschel *et al.* 2001; Murakami & Nakano 2002; Baxter *et al.* 2005). It has been shown that aquatic-terrestrial food-webs are often deeply intertwined and complex reciprocal interactions between the two ecosystems shape their communities and dynamics. The existence of trophic cascades across ecosystems is only one example of these complex interactions. The predation of fish on dragonfly larvae reduces the predation pressure on terrestrial plant pollinators and thus indirectly facilitates plant growth (Knight *et al.* 2005). In contrast, predation rates of fish on aquatic insects can be reduced in the presence of terrestrial arthropod subsidies and in turn grazing on periphytic algae by aquatic insects is increased (Nakano *et al.* 1999). However, although aquatic systems were found to receive higher amounts of spatial subsidies than terrestrial ecosystems, the contribution of spatial subsidies to carbon intake of the recipient food-web does not differ between the two systems (Bartels *et al.* 2012). The contribution of spatial subsidies to the food-webs of small islands has been integrated into the theory of island biogeography (Anderson & Wait 2001). In this ‘subsidized island biogeography’ it was hypothesized that spatial subsidies can increase species richness above an expected value of the species area curve, so that it explains the ‘small island effect’ (Niering 1963; Burns *et al.* 2009) in which species richness has a low or no variation below a certain size threshold. However, there is not much empirical support for this hypothesis (but see Barrett *et al.* 2003).

Despite the importance of fluxes between ecosystems, their significant magnitude and variation has been questioned by some authors. Only a few studies explicitly highlight the temporal variation of most spatial subsidies as an important co-variable (Stapp & Polis 2003; Nowlin *et al.* 2007; Wesner 2010; Leroux & Loreau 2012). Most spatial subsidies are resource pulses, which are short, rare periods of markedly increased resource availability, whose local effects vary in specificity and persistence (Yang *et al.* 2008). Nevertheless, the effect of timing, duration and frequency of spatial subsidies on recipient communities and food-webs is yet poorly studied (Richardson *et al.* 2010).

A few studies have investigated how deep the effects of spatial subsidies penetrate inland (Briers *et al.* 2005). For streams, a recent meta-analysis revealed that the lateral extent of spatial subsidies depends on the resource species and that the significant impact levels off after a few meters, so that effects of spatial subsidies mostly affect river banks but often contribute ~ 10 % of the food at a distance of 0.5 km (Muehlbauer *et al.* 2014). Studies quantifying the lateral export of PCB from streams via the consumption of aquatic insects by riparian spiders have found a lateral extent of max. 30 m, indicating that compound specific lateral transports cannot be deduced from more general methods and findings (Walters *et al.* 2008; Raikow *et al.* 2011). Similar studies on temperate islands find that the major impact of spatial subsidies on recipient communities is restricted to the intertidal zone, but the true distance of the impact might be species specific (Paetzold *et al.* 2008).

Considering the knowledge about spatial subsidies and allochthonous inputs that was gathered in ecological sciences during the last 35 years, it is becoming clearer and clearer that real food-webs do not have defined boundaries. Neighboring ecosystems are intertwined by trophic interactions to such an extent, that even their basic food-web dynamics are non-independent. Transitions between adjacent ecosystems are almost always gradual. On the other hand, ecosystems have characteristic attributes and measurable environmental factors, which make them identifiable within the landscape, so that autochthonous and allochthonous impacts and dynamics are not completely indistinguishable. Future studies have to quantify and describe the strength of both forces within explicit space and time between a diversity of ecosystems to better understand food-web dynamics in a complex mosaic at the landscape scale.



Together with the theoretical and empirical knowledge about food-web structure and dynamics, the methods to elucidate these ecological principles have developed. The basic unit within a food-web is a trophic interaction. Trophic interactions between organisms within ecosystem have been traditionally investigated by direct observations of feeding events and via gut content or fecal analysis. Since observations with mounted cameras or by researches *in situ* can only reveal a fraction of the possible feeding interactions and gut content analysis is impossible for animals with extra-intestinal digestion, DNA probing of gut content was developed. However, DNA analysis depends on species specific primers, which are sometimes difficult to design and require *a priori* knowledge about which species can be considered as prey (Sheppard & Harwood 2005; King *et al.* 2008). The most widely used technique to study food-web structure and dynamics today, is stable isotope analysis. Chemical elements occur in nature as an isotopic spectrum, with isotopes of the same elements having identical numbers of protons in their nucleus but variable numbers of neutrons. Isotopes of the same element have identical chemical properties but different mass numbers. Most elements have isotopes that are stable and isotopes, which are radioactive, i.e. they are unstable and spontaneously disintegrate. However, some elements, like phosphorus, have no stable isotopes. The elements that are most interesting for biologists are carbon (C), nitrogen (N), hydrogen (H), oxygen (O) and sulfur (S), which occur as the isotopes  $^{12}\text{C}/^{13}\text{C}$ ,  $^{14}\text{N}/^{15}\text{N}$ ,  $^1\text{H}/^2\text{H}$ ,  $^{16}\text{O}/^{18}\text{O}$  and  $^{32}\text{S}/^{34}\text{S}$ . In all of these elements, the heavier isotope is rarer in nature, in most cases accounting for only a thousandth of the total abundance of atoms of an element on planet earth. Due to their identical chemical properties, but different mass numbers the stable isotopes of an element undergo identical chemical reactions, but at a different rate. Thus, in some biochemical reactions, the stable isotopes of an element are contained in different proportions in the product than in the reactants. This process is called isotopic fractionation. In practice, the isotopic ratios of an element within a sample are compared to the isotopic ratio within a standard. For carbon, this standard is a marine limestone fossil, the Pee Dee Belemnite (PDB) and for nitrogen, atmospheric air is used as a standard. The isotopic signature ‘ $\delta$ ’ of a sample is calculated as:

$$\delta = \frac{R_{sa} - R_{std}}{R_{std}} \times 1000$$

$R_{sa}$  is the ratio of the sample and  $R_{std}$  is the ratio of the standard. The unit used is per mill (‰) (Lajtha & Michener 1994).

It was found that plants discriminate against the heavier  $^{13}\text{C}$  isotope in physical and biochemical processes. In all plants, the fractionation ( $\Delta$ ) of  $^{13}\text{C}$  due to slower diffusion rates at the plant leaf stomata is about 4 ‰. Since plants differ in their initial steps of carbon fixation, using different enzymes, the fractionation due to enzymatic reactions differ between  $\text{C}_3$ ,  $\text{C}_4$  and CAM plants. In  $\text{C}_3$  plants, the enzyme ribulose biphosphate carboxylase (rubisco) accounts for a fractionation of about 29 ‰.  $\text{CO}_2$  of atmospheric air has a  $\delta^{13}\text{C}$  of  $\sim -8$  ‰, resulting in a theoretical value of  $-41$  ‰. But the real signature of  $\delta^{13}\text{C}$  in plants depends on the rates of supply and reaction within  $\text{C}_3$  plants, so that signatures found in the field are around  $-27$  ‰.  $\text{C}_4$  plants fix carbon with the enzyme phosphoenolpyruvate (PEP) carboxylase, which accounts for around 6 ‰ of the fractionation, so that  $\delta^{13}\text{C}$  signatures of  $\text{C}_4$  plants are around  $-14$  ‰. CAM plants that switch between  $\text{C}_4$  and  $\text{C}_3$  cycle at day and night have  $^{13}\text{C}$  signatures around  $-11$  ‰ (Lajtha & Marshall 1994).

It has further been found that  $\delta^{13}\text{C}$  undergoes little or no fractionation when transported up the food-chain (DeNiro & Epstein 1978), while  $\delta^{15}\text{N}$  signatures are enriched at each trophic level (Deniro & Epstein 1981; Minagawa & Wada 1984). Thus the  $\delta^{13}\text{C}$  signatures of consumers are similar to those of their prey, while their  $\delta^{15}\text{N}$  signatures are enriched relative to their prey. Minagawa and Wada found an average fractionation between trophic levels of 3.4 ‰ with a standard variation of 1.1 ‰ investigating a diversity of different animals. This value was later confirmed for fishes in lakes (Post 2002b) but subsequent meta-analyses found different values of enrichment of  $^{15}\text{N}$  per trophic level, depending on habitat (Vanderklift & Ponsard 2003) and type of organism (McCutchan *et al.* 2003). These meta-analyses also found fractionations of  $^{13}\text{C}$  per trophic level different from 0.0 ‰, with values between 0.5 ‰ but high variation from depletion in  $\delta^{13}\text{C}$  to enrichment  $> 1$  ‰ per trophic level.

Consequently, the isotopic fractionation between trophic interactions within a food-web has been exploited by ecologists to investigate feeding links, trophic structure and dynamics in natural systems. More and more differences in  $\delta^{13}\text{C}$  signatures between habitats and diet types were revealed and subsequently, studies multiplied, which investigated animals feeding on them. In aquatic food-webs it was found, that benthic algae are enriched in  $^{13}\text{C}$  compared to phytoplankton (France 1995; Doi *et al.* 2009). As such terrestrial plants mostly lie between benthic and pelagic  $\delta^{13}\text{C}$  signatures and thus, aquatic signatures can be traced in terrestrial food webs and vice versa (Cloern *et al.* 2002; Lancaster *et al.* 2008). Meanwhile a growing number of models have emerged, which aid ecologists in estimating the proportional contribution of multiple diets to the total intake of a consumer (Phillips & Gregg 2003; Semmens & Moore 2008). However, it has become evident that  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures in natural systems co-vary with other factors than trophic position, which interfere with a definite identification of diet organisms and their proportional contribution (reviewed in Boecklen *et al.* 2011).

Nonetheless, stable isotope analyses are the most promising approach today in identifying and quantifying trophic interactions between species and food-web compartments, provided the included diet types vary in their isotopic signature. The enrichment in  $\delta^{15}\text{N}$  during trophic interactions can provide a continuous measure of food-chain length, which integrates quantities of different diet types on different trophic levels for omnivorous consumers (Rickers *et al.* 2006; Wise *et al.* 2006). Therefore, stable isotope analyses are ideal for studying large scale food-web parameters, without having to analyze every single trophic interaction to achieve the concluding emergent level of organization. Many of the studies cited in the sections above, which investigated cross-ecosystem fluxes of organisms and allochthonous inputs (Barrett *et al.* 2005; Paetzold *et al.* 2006), as well as those investigating patterns of food-chain length (Post *et al.* 2000b; Takimoto *et al.* 2008) were conducted using stable isotope analysis. Additionally, natural abundances of  $^{13}\text{C}$  and  $^{15}\text{N}$  have been used to investigate the niche breadth of animals (Bearhop *et al.* 2004; Layman *et al.* 2007; Newsome *et al.* 2007) and to trace the migration of animals (Hobson 1999). For coccinellid beetles a diet shift during habitat change was demonstrated with a shift in  $\delta^{13}\text{C}$  signatures within different body parts (Gratton & Forbes 2006).

In conclusion, the evidence for a systematic variation of food-web properties with ecosystem size is scarce for terrestrial systems and the contribution of spatial subsidies has not been related to area in these systems. Furthermore, it is still questionable, if the stable isotope approach can be used to identify large scale patterns like an FCL-area relationship in diverse, previously unexplored communities. I therefore investigate small man-made islands of varying size in two gravel pit lakes with a stable isotope approach to test for a food-chain area relationship in a diverse arthropod community. I chose ground beetles and spiders as focal organisms, since both arthropod groups are well studied and have a striking background as model organisms in island biogeographical studies and

analyses of the contribution of aquatic subsidies to terrestrial food webs. I furthermore test for a systematic variation in the contribution of spatial subsidies to island food webs.

According to previous studies, it can be expected that,

- food-chain length increases with island area
- some terrestrial consumers feed on aquatic subsidies.
- due to the low productivity on the larger sandy man-made islands, species richness and abundances should be higher in gravel-shore habitats than in the central island habitats.
- The contribution of aquatic subsidies to the terrestrial food-web should decrease with increasing island area.

The small size and the close vicinity of the islands to the terrestrial mainland suggest a strong prevalence of mass effects in the community assembly of the lake-islands. The island communities should therefore

- be similar to that on the mainland
- be less subjected to species sorting and hence niche differentiation should be low

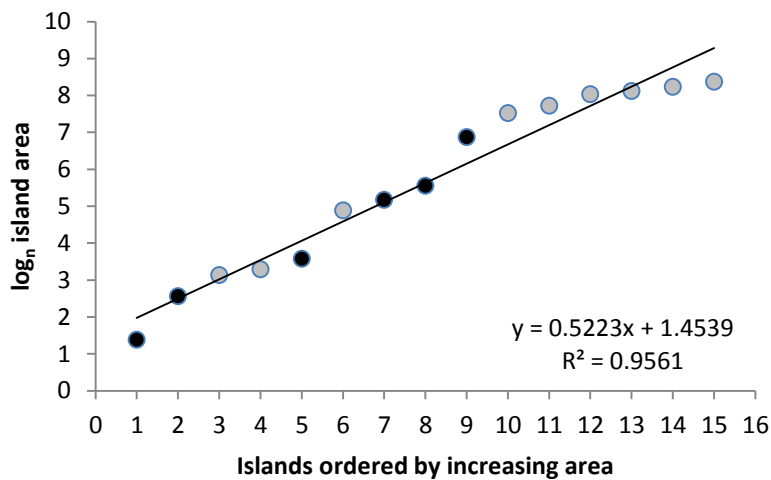
## Materials and Methods

### *Study site*

The study site covers sixteen islands of varying topology and four mainland sites at two adjacent gravel pit lakes in the Lower Rhine area, near Wesel in North Rhine-Westphalia, Germany, the “Diersfordter Waldsee” (6°32'E, 51°41'N) and the “Brüggehofsee” (6°30'46"E, 51°42'20"N). The islands were created by deposition of waste-material - sand, loam and gravel - during the gravel mining process between 1997 and 2003, i.e. at the sampling date they were ~ 10 years old. We also included an island of 0.1 ha that was established in spring 2010. The islands spanned sizes between 4 m<sup>2</sup> and 4400 m<sup>2</sup> in a log-linear fashion (Fig. M1; Tab. M1). Except for the recently created island, which was far more isolated (163 m shortest distance to the mainland) the mean distance of islands to the mainland was 20 m and the mean distance to the nearest island 6 m.

Habitat types ranged from wet fen meadows, with *Juncus* spp. dominating on smaller islands to sparsely vegetated, sandy xeric grasslands and bare sand flats on larger islands, bordered by gravel shores with interspersed *Juncus* spp. stands and *Equisetum* spp. The mainland sites were soft-wood (*Salix* sp., *Alnus* sp.) and hard-wood floodplain forests, sandy xeric grassland and woodland with sandy shore. Larger islands were annually grazed by sheep to prevent soft-wood forest formation by *Salix* sp. seedlings. The main vegetation type of the islands in the Diersfordter Waldsee was that of dry sandy xeric grasslands and dry calcereous grasslands with a typically low vegetation of Poaceae and Trifolieae, dry resistant mosses, *Sedum* spp. and *Salix* sp. seedlings and *Cirsium* spp. One of the larger islands (“D6”) contained a freshwater pond, which fell dry in summer.

The two lake systems were connected to the river Rhine via groundwater. Thus, lake water levels co-varied with water levels of the Rhine with a delay of several weeks. Restoration plans primarily envisaged the temporary inundation of the deposited islands, when water levels increase in the Rhine due to increasing precipitation in winter or snow melt in early spring. However, in 2003 when the restoration of the lake islands was finished, water gauges of the Rhine were on a record low, (111 cm in Wesel, 81 cm in Cologne). Since then no high-waters occurred and accordingly water levels never increased as much as to inundate the islands in the Diersfordter Waldsee. Some of the smaller islands in the Brüggehofsee were inundated during the remaining variation of water levels ( $\pm 60$  cm). These islands were not included in the sixteen islands, sampled in 2010. Between 2009 and 2010 water levels of the Diersfordter Waldsee changed no more than 25 cm. Due to the method of island creation via deposition of gravel mining residues, island elevation significantly increased with island area from ~ 0.2 m for the small islands up to ~ 0.7 m for the larger islands in the Diersfordter Waldsee. One of the smaller islands in the Diersfordter Waldsee with an area of ~ 130 m<sup>2</sup> and a larger island in the Brüggehofsee of ~ 1000 m<sup>2</sup> had been raised to higher elevations of ~ 1.3 to ~ 1.8 m. The other small islands in the Diersfordter Waldsee had an elevation of ~ 0.15 m and flat angles of elevation between 5° and 9°. Thus they were partly washed by wave action in storms and windy weather. Mean angles of elevation were steeper, between 15° and 24° for larger islands. On larger islands, right-angled erosion folds were occasionally interspersed into the otherwise steadily rising island shores, so that movement of organisms between shore and island center was predominantly barrier free. Occasionally, movement barriers occurred on small islands in the Brüggehofsee, between muddy island edges fallen dry and dense stands of *Juncus* spp. Some of the smaller islands were used by waterfowl like seagulls and anserine birds as resting places, while larger islands were occasionally used as nesting sites. As a consequence some small islands were more densely covered with bird feces than others. These islands are referred to as ‘bird islands’ hereafter.



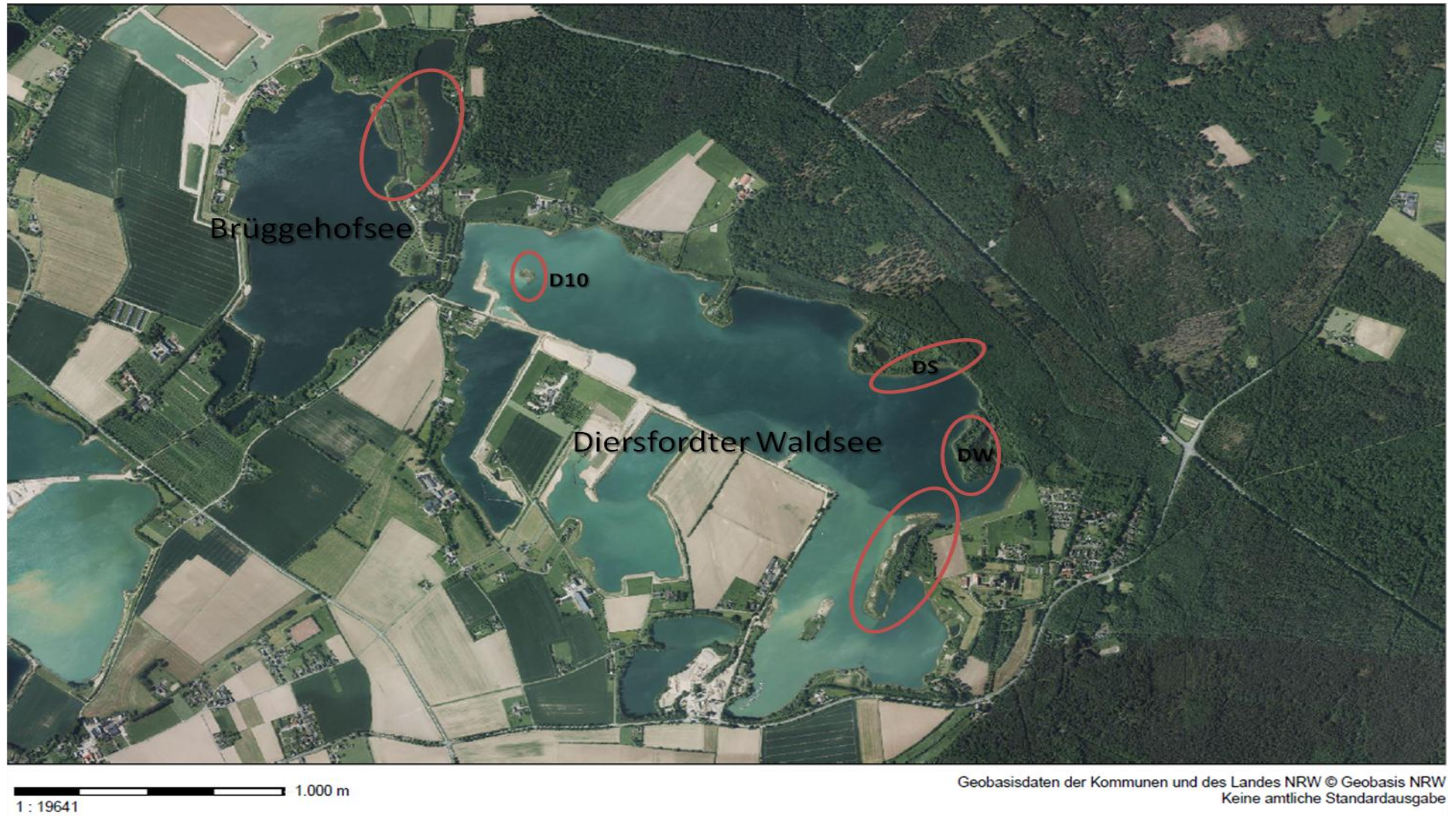
**Fig. M1** log-linear increase of island size; black dots denote islands of the Brüggehofsee, grey dots denote islands of the Diersfordter Waldsee

#### *Sampling procedure and identification*

The activity density and species composition of ground beetles (Carabidae) and vagrant spiders were sampled with pitfall traps on all 16 islands from the 1<sup>st</sup> of June, 2010 to the 14<sup>th</sup> of June, 2010. Density and species richness of these organisms seasonally peak at this time (Thiele 1977). Depending on island size and topology, between 3 and 12 pitfall traps were set up per island in a zonal design. The pitfall traps consisted of 375 ml glass jars, 55 mm in diameter, filled to  $\frac{1}{3}$  with saturated salt solution ( $\sim 350 \text{ kg/m}^3 \text{ NaCl}$ ) and a custom made flat polypropylene ring screwed on to the jars prevented sand and other materials from falling in. Additionally, the flat ring had an overhanging edge on the interior of the jar opening, so that trapped insects and spiders were further restrained from climbing out. In this design, four transects were placed on each island. Four traps were placed directly at the shore (zone A), with a distance of at least 1 m to the water line, to prevent washing out. Four traps were placed in a distance of 2.8 m to the trap in the shore zone (which was the distance between the center and the shore of the smallest island with this design; zone B) and on larger islands, four traps in the center line (zone C). Zone B was set up to explore gradients of species occurrences between the shore and the islands centre. The design described above was also used on mainland sites, so that larger islands and mainland sites had a maximum of 12 traps. Altogether the zonal design was applied to 13 of 20 sites. 202 Traps were used for a single survey, with an active catching period of 14 days (2828 trap days). On eleven islands, six different plant species each were collected by hand. Detritus was collected at different places on eight islands. Aquatic insects, algae and submerged macrophytes were also collected by hand from both lakes. Aquatic insects could also be retrieved from pitfall traps placed at the shores. Arthropods retrieved from the field were assorted to pitfall identity and animal order, rinsed and stored in distilled water at  $-18 \text{ }^\circ\text{C}$ . All spiders were identified to the species level, using the keys of Roberts (1987; 2001) and Nentwig *et al.* (2003). Ground beetles were identified to the species level, using the key of Freude *et al.* (2006). Individuals of dimorphic species were checked for their actual wing status during identification.



**Fig. M2** Top view of the lower Rhine area between Xanten and Wesel, showing the location of the study area



**Fig. M3** Top view of the study area, showing the two gravel-pit lakes and the location of the islands archipelagos and the exact location of Island D10 and the mainland sites DS and DW



**Fig. M4** Exact location of the islands in the Diersfordter Waldsee, including the mainland site DF





**Fig M5** Exact location of the islands in the Brüggehofsee, including the mainland site BF

**Tab. M1** Information on island (Dx, Bx) and mainland sites (BF, DF, DS, DW) trap numbers, island area, perimeter to area ratios (p/a – ratios), mean elevation in meters and shore slope (angle in degrees)

Island	Number of traps	Island area (m <sup>2</sup> )	p/a ratio	Perimeter (m)	Mean elevation (m)	Shore slope (deg)
<b>BF</b>	12	---	--	--	--	--
<b>DF</b>	12	---	--	--	--	--
<b>DS</b>	12	---	--	--	--	--
<b>DW</b>	12	---	--	--	--	--
<b>B1</b>	3	4	2	8	0.30	--
<b>B11B</b>	3	13	1.15	15	0.15	--
<b>D1</b>	8	23	0.91	21	0.18 ± 0.06	9.0° ± 1.9°
<b>D2</b>	8	27	0.81	22	0.12 ± 0.04	5.7° ± 1.4°
<b>B11A</b>	3	36	0.56	20	0.15	--
<b>D3</b>	12	133	0.38	50	1.05 ± 0.32	23.7° ± 4.7°
<b>B8</b>	12	177	0.38	67	0.40	--
<b>B12</b>	12	258	0.27	70	0.25	--
<b>B2</b>	9	970	0.20	193	1.8	--
<b>D10</b>	12	1850	0.09	170	0.25 ± 0.05	10.7° ± 1.6°
<b>D4</b>	12	2263	0.09	213	0.27 ± 0.03	15.6° ± 4.0°
<b>D6</b>	12	3096	0.08	251	0.55 ± 0.21	22.9° ± 11.9°
<b>D8</b>	12	3375	0.09	309	0.58 ± 0.06	20.0° ± 2.5°
<b>D5</b>	12	3763	0.09	366	0.33 ± 0.12	12.5° ± 2.8°
<b>D7</b>	12	4340	0.09	425	0.75 ± 0.10	23.6° ± 7.0°

### *Stable isotope analyses*

After identification and counting of ground beetles and spiders and sorting potential terrestrial and aquatic prey species, species for stable isotope analyses were selected. Species, chosen for stable isotope analysis included every spider species on every island with a reasonable population density, but also spider species with only one or two individuals on an island, if densities of that species were high at other sites. Ground beetle species were also chosen according to their activity density, but also according to the zone they were most active in. Species predominantly occurring in the shore zone were always chosen, since their potential to utilize aquatic subsidies was considerably high.

At least five (but mostly six) ground beetle or spider individuals of a species, as well as six plant species of each island, if possible, were chosen for stable isotope analysis.

Prior to the sample preparation for stable isotope analyses, the selected ground beetles, spiders, aquatic insects, detritus and plant materials were dried at 60 °C for at least 48 h. After drying, individuals were weighed and stored in a desiccator. Subsequently, all animals were ground to homogenized powder in an agate mortar. Plants and Detritus were ground to homogenized powder in a ball mill (MM 400; RETSCH; Haan, Germany). Between 1.0 and 1.5 mg of dry animal powder were weighed into a tin capsule for each individual. Organisms that perfectly fitted this range of weight were packed into tin capsules as whole. If animal individuals did not meet the minimum weight requirements, individuals were lumped together until the optimum weight (1.25 mg) was met. This was the case for collembolans, ants of the genus *Lasius* and *Themnotorax*, dwarf spiders (Linyphiidae; *Erigone* spp., *Oedothorax* spp., *Meinotea* spp., ant-like flower beetles (Anthicidae) and smaller ground beetle species (e.g. *Dyschirius thoracicus*). Stable isotope analysis of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  was performed at the Stable Isotope Facility of the University of Davis, California. Algae and zooplankton were subjected to acid fumigation, using the method of Harris *et al.* (2001) to remove heavily enriched inorganic

carbonate with  $\delta^{13}\text{C}$  values close to 0 ‰, which would potentially distort the isotopic signals resulting from the diet of the analyzed organisms.

### *Statistical analysis*

Species area relationships (SAR) were tested for significant linear correlations in the log-log form, and the widely used power law models of the form  $S = cA^z$  (Preston 1960) were calculated for all spider- and all ground beetle species, as well as for the subgroups vagrant spiders, Lycosidae, Linyphiidae, phytophagous and non-phytophagous ground beetles, riparian and non-riparian ground beetles. Rarefaction of species richness was performed with the package *vegan* (Oksanen *et al.* 2013) for R (RCore 2014), using the function `specpool`. The second order Jackknife algorithm was chosen as estimator, because it is abundance based and less sensitive to sampling coverage and sampling grain than other estimators (Brose *et al.* 2003; Hortal *et al.* 2006). Density area relationships (dAR) (Connor *et al.* 2000) were tested and calculated from catches per trap numbers in the same manner. Catches per trap (CPT) was chosen as a density measure to correct for differing numbers of pitfall traps between islands and pitfall failures. CPT was the total number of catches from valid pitfall traps on an island, divided by the number of these valid pitfall traps. Ground beetle species were categorized into subgroups of riparian and non-riparian or phytophagous and non-phytophagous beetles, following habitat requirements specified in Freude *et al.* (2006) and Turin *et al.* (2000). The class ‘vagrant spiders’ was introduced into the analysis to exclude net-building spiders and sedentary crab spiders (Thomisidae) which are generally unlikely to be caught in pitfall traps in representative densities. The class vagrant spiders contained non-net building hunters of the families Lycosidae, Gnaphosidae, Clubionidae, Liocranidae, Corrinidae, Salticidae, Pisauridae, Philodromidae and adult individuals of the Tetragnathid *Pachygnatha clercki* (Sundevall, 1823). Zonal differences between species richness and activity density were analyzed using one-way ANOVA. The edge response, i.e. shore affinity, of each ground beetle and spider species was calculated as log response ratio of the sum of individuals caught at all sites ( $N=13$ ) in zone A and zone C ( $\ln(I_A/I_C)$ ). Many riparian ground beetles were severely restricted to shore habitats and despite high positive values for  $I_A$  they had values of  $I_C = 0$ , causing the log response ratios of these species to be undefined. Since these zero values are definitely meaningful, representing the strongest edge response possible, zero values were replaced by the lowest possible activity density ( $I_C = 1$ ) to gain an appropriate estimate of the true log response ratios. Furthermore, an arbitrary threshold-density of  $> 5$  individuals for a calculation of edge responses of ground beetles and spiders was chosen. Altogether, edge response values were calculated for 24 spider and 26 ground beetle species. Literature values for the shade and drought preferences of spider species were taken from Entling *et al.* (2007).

When niche properties are available as continuous or relative measurement variables, the variability of niche property values can be expected to increase with area purely statistically by random sampling. As more species randomly accumulate in larger areas, their niche properties can also be expected to show a higher variation than those of smaller randomly assembled communities in smaller areas. Excluding random sampling effects becomes increasingly difficult the more limiting habitat types and limiting niche properties are available within larger areas. The easiest approach would only become available if there is a single limiting environmental factor that increases with area. The mean niche property value of the community would then systematically converge according to the limiting environmental factor with increasing area. These conditions rarely apply to available literature data or to the size range of islands and fragments surveyed in most studies. However, even the most simple and monotonous habitat space can be divided into two environmental types, central habitat and ‘edge’. Even the most simple and monotonous habitat area more or less changes in environmental conditions towards the edge, depending on the steepness of the environmental gradient, between the focal habitat patch and the surrounding environment (Cadenasso *et al.* 2003). As area decreases, the relative

proportion of edge habitat within a patch increases. If the smallest patch solely consists of edge habitat, it is readily understandable, how simply by increasing patch area the available amount of distinct habitats and the number of adapted species therein would increase. Indeed it has been argued, that some observed effects of area are in fact edge effects (Fletcher *et al.* 2007), although changing terms, the true underlying mechanism is habitat heterogeneity. If the transition from edge to center habitat is accompanied by the gradient of a single environmental parameter, this would meet the definition of ‘heterogeneity’ by Li and Reynolds (1995), who wrote: “*Heterogeneity is thus defined as the complexity and/or variability of a system property in space and/or time.*”

Mean values of shade and drought preferences for island communities were calculated as:

$$\bar{Y}_j = \frac{\sum_{i=1}^n Y_{ij}}{S_j}$$

Where  $Y$  is the preference value of a species  $i$  on island  $j$  and  $S$  is the species richness on island  $j$ .

Nestedness temperatures of spiders, ground beetles and their subgroups were calculated from the same dataset used for the analysis of SARs, with the software NESTCALC (Atmar & Patterson 1993; 1995), using 1000 Monte-Carlo runs to calculate significance levels. All linear statistics were performed using *STATISTICA* (StatSoft 2007).

The similarity of community composition between islands and mainland, as well as between the two lake systems was analyzed using ANOSIM (Clarke 1993), included in the software package PAST (Hammer *et al.* 2001). As measure of similarity, Jaccard distance was used in this analysis (Jaccard 1912).

Distribution of ground beetle wing development in the islands system was analyzed using a Mann-Whitney-U test.

It was tested, if the co-occurrence within each group of ground beetles and spiders was significantly different from random assemblages, using the measures C-Score (Stone & Roberts 1990) and Checkerboard score (Diamond 1975a) in the software ECOSim (Gotelli & Entsminger 2009). The sequential swap algorithm was used to calculate > 10,000 random matrices from the original matrix (Gotelli & Entsminger 2003).

To explore the species distribution along axes of environmental factors, a canonical correspondence analysis (CCA) was performed with the software CANOCO 4.5 (Ter Braak 1988). It was performed by down-weighting rare species and testing for the significance of the distributions using > 1000 Monte-Carlo runs. The data used was resolved to single pitfall traps. Each pitfall trap was categorized into estimates of binary habitat categories, i.e. either 0 or 1 were assigned to the habitat categories ‘gravel shore’ or ‘shore vegetation’. Furthermore vegetation density was estimated by analyzing photo material recorded at the time of the sampling in 2010, assigning levels from 0 to 3. Humidity and distance to edge were measured variables. These methods were applied to datasets of ground beetles, vagrant spiders and Linyphiidae.

To gain estimates about the major food of ground beetles and spiders, results of the stable isotope analyses were used in the mixing model MixSIR (Semmens & Moore 2008). From two small islands, three potential prey organisms entered the model. From all other islands, five potential prey organisms or plants were used. To gain insight, how outcomes of the mixing model varied with assumptions about the fractionation of  $^{15}\text{N}$  and  $^{13}\text{C}$  between trophic levels, the proportion of food intake for each species analyzed was calculated with three different enrichment factors. I used the three most

prominent mean values for the fractionation of  $^{15}\text{N}$  and  $^{13}\text{C}$  per trophic level published, that also reported standard deviations. The first were the enrichment factors, published by Post (2002b), hence called POST. Their value and standard deviation for the  $\Delta^{15}\text{N}$  enrichment factor are similar to the original values published by Minagawa and Wada (1984). The second was the enrichment factor of McCutchan *et al.* (2003)(MCC), and the third was the enrichment factor proposed by Spence and Rosenheim (2005)(SR).

**Tab. M2** Mean fractionation of  $^{15}\text{N}$  and  $^{13}\text{C}$  per trophic level with standard deviations (STD) published by different Authors

Authors	$\Delta^{15}\text{N}$	STD $\Delta^{15}\text{N}$	$\Delta^{13}\text{C}$	STD $\Delta^{13}\text{C}$
POST	3.40	1.00	0.40	1.30
MCC	2.30	0.18	0.50	0.13
SR	1.88	0.37	-0.53	0.26

For ground beetle species with low  $^{15}\text{N}$  values and potential herbivores, mean values for detritus and plants were included in the model. For ground beetle and spiders species with  $\delta^{15}\text{N} > (\text{plant } \delta^{15}\text{N} + 3.4 \text{ ‰})$ , only animals were used as prey in the model. On most islands the ant species *Lasius niger* was used as a potential prey item. On the smallest island of the Brüggehofsee (B1) the beetle species *Chaetartria seminulum* (Herbst, 1797) from the family Hydrophilidae were used as a prey species due to their high abundance. Beetle larvae from the family Haliplidae were used as aquatic prey item on small islands in the Brüggehofsee. In the Diersfordter Waldsee, mayflies were used as aquatic prey. Data on the isotopic signature of collembolans were only available for two larger islands, D7 and D8. For the other larger islands, the mudhopper species *Tetrix* sp. was used. On islands D6 and D7, two different prey assemblages were used in models, due to the high species richness. In an alternative scenario, woodlice (*Porcellio* sp.) and pill-bugs (*Armadillidium* sp.) were used as prey items for larger spiders. Also ground beetles like *Stenolophus teutonius*, *Nebria salina*, *Omophron limbatum* were used as prey species for spiders in MixSIR models.

**Tab. M3** Organisms used as prey in MixSIR models; Prey 4 and 5 were represented by either detritus or plants for obligate herbivorous species or by phytophagous beetles and other more basal beetle species for spiders

Island	Prey 1	Prey 2	Aquatic prey	Prey 4	Prey 5
B1	<i>C. seminulum</i>	Snails	Haliplidae	<i>A. duftschmidi</i>	<i>E. riparius</i>
B8	<i>L. niger</i>	Snails / <i>S. teutonius</i>	Haliplidae	<i>O. retusus</i>	Plants / <i>P. anthracinus</i>
D4	<i>L. niger</i>	<i>Tetrix</i> sp.	Mayflies	Detritus/phytophagous	Plants / <i>S. teutonius</i>
D5	<i>L. niger</i>	<i>Tetrix</i> sp.	Mayflies	Detritus/ phytophagous	Plants / <i>N. salina</i>
D6	<i>L. niger</i>	<i>Tetrix</i> sp.	Mayflies	Detritus/ phytophagous	Plants / <i>S. teutonius</i>
D6/2	<i>Porcellio</i> sp.	<i>Armadillidium</i> sp.	<i>O. limbatum</i>	<i>C. hybrida</i>	<i>N. salina</i>
D7	<i>L. niger</i>	Collembola	Mayflies	Detritus/ phytophagous	Plants / <i>C. seminulum</i>
D7/2	<i>L. niger</i>	Collembola	Mayflies	phytophagous	<i>O. limbatum</i>
D8	<i>L. niger</i>	Collembola	Mayflies	Detritus/ phytophagous	Plants / Cicadae

Food chain length was calculated for 11 islands using the equation  $\text{TL} = ((\delta^{15}\text{N}_{\text{pred}} - \delta^{15}\text{N}_{\text{base}}) + \lambda) / \Delta\text{N}$ , where TL is the trophic level,  $\delta^{15}\text{N}_{\text{pred}}$  is the  $^{15}\text{N}$  signature of the predator (ground beetle or spider) and  $\delta^{15}\text{N}_{\text{base}}$  is the  $^{15}\text{N}$  signature of the food-chain base line and  $\Delta\text{N}$  is the average enrichment factor per trophic level (Post 2002a). Although enrichment factors lower than 3.4 ‰ were reported for trophic interactions of terrestrial invertebrates (Vanderklift & Ponsard 2003), in our study the enrichment factor of the most common interaction between the phytophagous ground beetle *Amara aenea* (De

Geer, 1774) and the lycosid spider *Xerolycosa miniata* (C.L. Koch, 1834) was indeed  $\sim 3.4$  ‰. Since this study focused on the relationship between area and food chain length, the true enrichment factor was of minor importance, because the relationship will not be changed by different fractionations between trophic levels, provided the same fractionation values are used throughout the model.  $\lambda$  is a correction factor to assign the correct trophic level. On most small islands, plants were used as baseline ( $\lambda=1$ ). On one small island lacking plants, detritus was used as baseline ( $\lambda=1$ ). On larger islands, herbivores were used as baseline ( $\lambda=2$ ). As baseline herbivores the strictly phytophagous ground beetles *Amara aenea* (De Geer, 1774) and *Harpalus affinis* (Schrank, 1781) were chosen. The latter was categorized as phytophagous due to the overlap of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures of *H. affinis* and *A. aenea* according to the results of stable isotope analyses, although *H. affinis* is sometimes considered to be polyphagous. However, its predominant feeding on legume crops and plant seeds was confirmed in many different habitats (Sunderland *et al.* 1995).

The niche width of animals in isotopic space (Bearhop *et al.* 2004; Newsome *et al.* 2007), spiders and aquatic insects was analyzed using the package SIBER (Jackson *et al.* 2011) with the statistical software R (RCore 2014). Total Area (TA) measures the total area of the convex hull (contour line) of all individuals of a group within isotopic space (Layman *et al.* 2007). The standard ellipse is the measure of variation of bivariate data, similar to the standard deviation SD in univariate data. Niche overlap was measured using the standard ellipse area (SEA). SEAc is the corrected formula of SEA for small sample sizes.

## Results

The majority of all animals caught in pitfall traps in terms of activity density were predacious arthropods. Disregarding ants, the predacious arthropod groups with the highest activity densities were spiders (3194 individuals) and ground beetles (Carabidae; 2083 individuals). These two arthropod groups showed different distributions of activity density between mainland sites and islands. While 84 % of all ground beetle individuals were found on islands, the fraction of spiders found on islands was 69.8 %. The number of ground beetles caught per trap was also higher on islands, while catches per trap were higher on mainland sites for spiders.

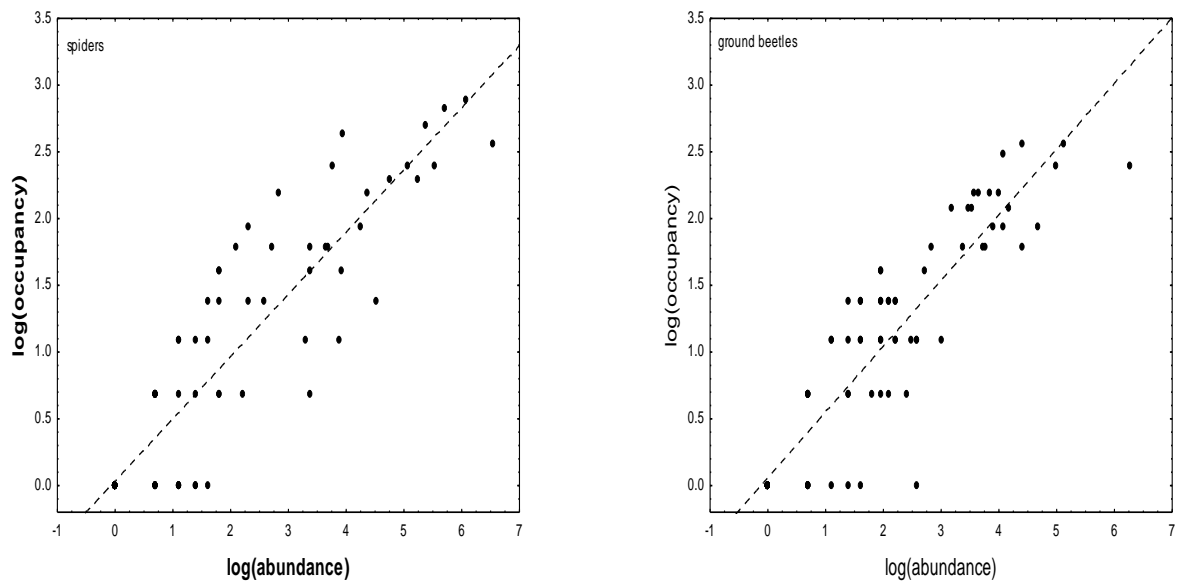
Although in both of these arthropod groups ~25 % of the species occurred exclusively on mainland sites, an analysis of similarity (ANOSIM) revealed that Jaccard similarity within groups of island and mainland sites was not significantly different from Jaccard similarity between groups of islands and mainland sites, i.e. that the community composition on mainland sites was not less similar to the composition of islands than island community compositions were to each other (Tab.1).

**Tab.1:** Results of ANOSIM, testing for significant dissimilarities between island and mainland community composition (Jaccard distance).  $r_w$  = mean rank within groups;  $r_b$  = mean rank between groups;  $p$  = significance level = probability that communities were perfectly similar; level of  $R$  (up to 1) signifies degree of dissimilarity;  $p < 0.05$  denotes significant community dissimilarity

Arthropod group	$r_w$	$r_b$	$R$	significance ( $p$ )
Ground beetles	89.7	107.0	0.18	0.11 (ns)
Spiders	98.8	89.0	-0.10	0.70 (ns)

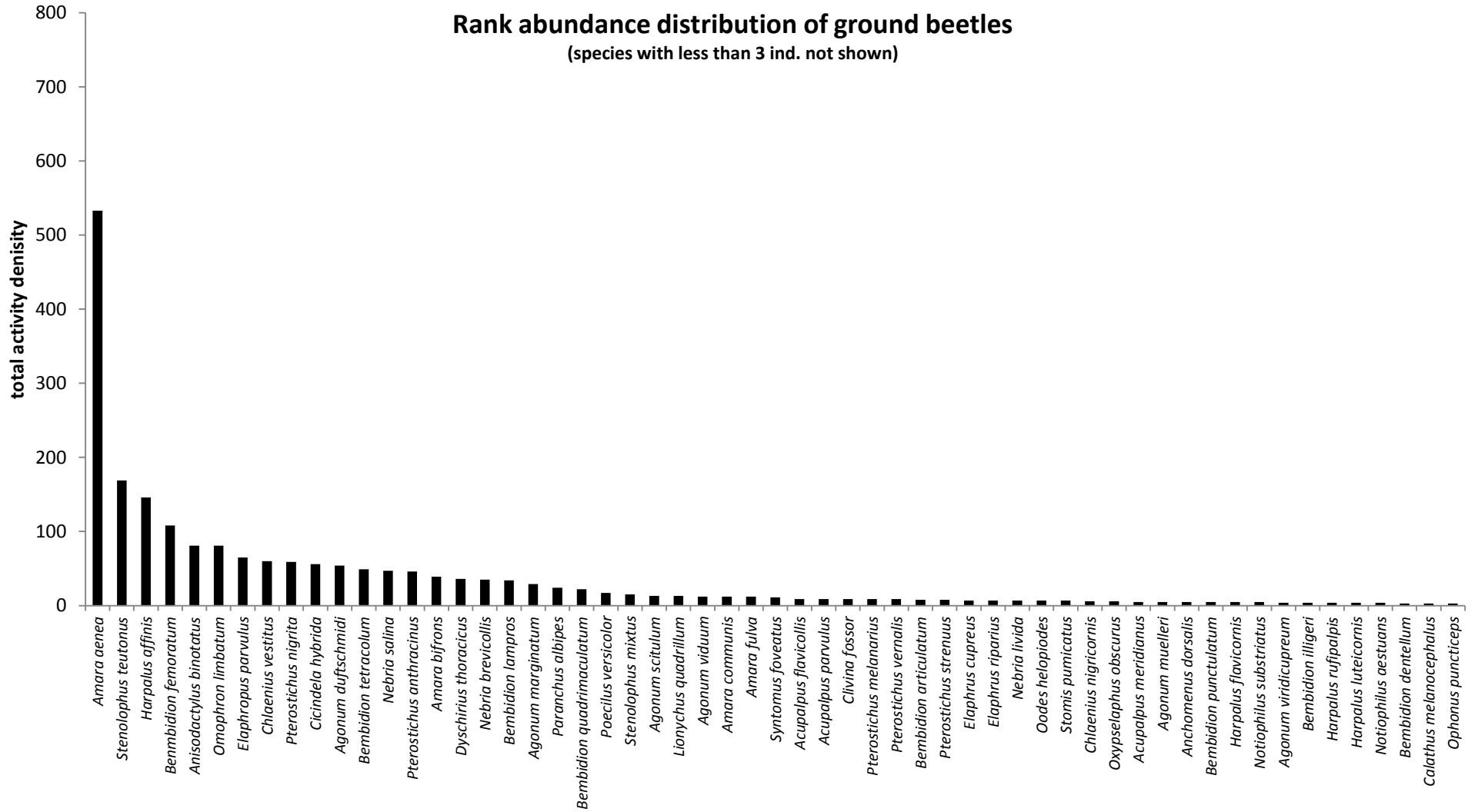
Spiders caught in pitfall traps were represented by 93 species from 48 genera and 14 families. Wolf spiders (Lycosidae) were the dominant spider family, representing 67.6 % of the catch. The remaining larger fractions were represented by money spiders (Linyphiidae; 18.3 %), ground spiders (Gnaphosidae; 6.1 %) and long-jawed orb weavers (Tetragnathidae; 4.3 %), i.e. these four spider families represented > 95 % of the catch. The most common spider species were wolf spiders. *Xerolycosa miniata* (C.L. Koch, 1834) was the most common in terms of activity density, while the most widespread species in the studied system (and the 2<sup>nd</sup> most abundant) was *Arctosa leopardus* (Sundevall, 1833). Also common and widespread were the wolf spiders *Trochosa ruricola* (De Geer, 1778), *Pardosa prativaga* (L. Koch, 1870) and the money spider *Erigone dentipalpis* (Wider, 1834) while the ground spider *Trachyzelotes pedestris* (C.L. Koch, 1837) and the wolf spider *Piratula hygrophila* (Thorell, 1872) were abundant, but their occurrence was restricted to a single mainland site. Widespread but less common were *Pachygnatha* spp. (Tetragnathidae) and *Oedothorax* spp. (Linyphiidae). The most species-rich genus was *Pardosa* (Lycosidae), representing 10 species. Six species were members of the genus *Clubiona* (Clubionidae), four species of the genus *Erigone* (Linyphiidae) and three species in each case were members of the genera *Arctosa* (Lycosidae), *Piratula* (Lycosidae), *Trochosa* (Lycosidae), *Oedothorax* (Linyphiidae), *Tenuiphantes* (Linyphiidae) and *Pachygnatha* (Tetragnathidae). 74.5 % of all spiders caught were males, but interspecific variation of male/female ratios was high, and ranged from 9:1 in *Erigone dentipalpis* (Sundevall, 1830) to 1:9 in *Arctosa perita* (Latreille, 1799). Nevertheless, in the majority of spider species males dominated the catch. The number of juveniles caught was negligibly low so that in fact > 99 % of all spiders caught were adults.

Ground beetles in pitfall traps were represented by 84 species from 33 genera and 14 subfamilies. The dominant subfamilies were the Pterostichinae (36.4 %), the Harpalinae (21,9 %) and the Trechinae (14.6 %). By far the most abundant ground beetle species was *Amara aenea* (De Geer, 1774), commonly known as the common sun beetle, followed by *Harpalus affinis* (Schrank, 1781), although the species *Anisodactylus binotatus* (Fabricius, 1787), *Stenolophus teutonius* (Schrank, 1781) and *Chlaenius vestitus* (Paykull, 1790) were more widely distributed throughout the system. The most species-rich genus was *Bembidion*, comprising 12 species. Many other species were members of the genera *Pterostichus* (nine species), *Agonum* (eight species), *Harpalus* (seven species) and *Amara* (six species). Site occupancy was positively related to total abundance in both groups (spiders:  $y = 0.04 + 0.47*x$ ;  $r = 0.91$ ;  $r^2 = 0.83$ ;  $p < 0.001$ ; ground beetles:  $y = 0.06 + 0.49*x$ ;  $r = 0.90$ ;  $r^2 = 0.81$ ;  $p < 0.001$ ), but common spider species reached higher occupancies (Fig. 1). Rank abundance distributions (RAD) and ranked species occupancy curves (RSOC) are shown in Fig. 2-5. A full species - island matrix of ground beetles and spiders is given in Appendix A.

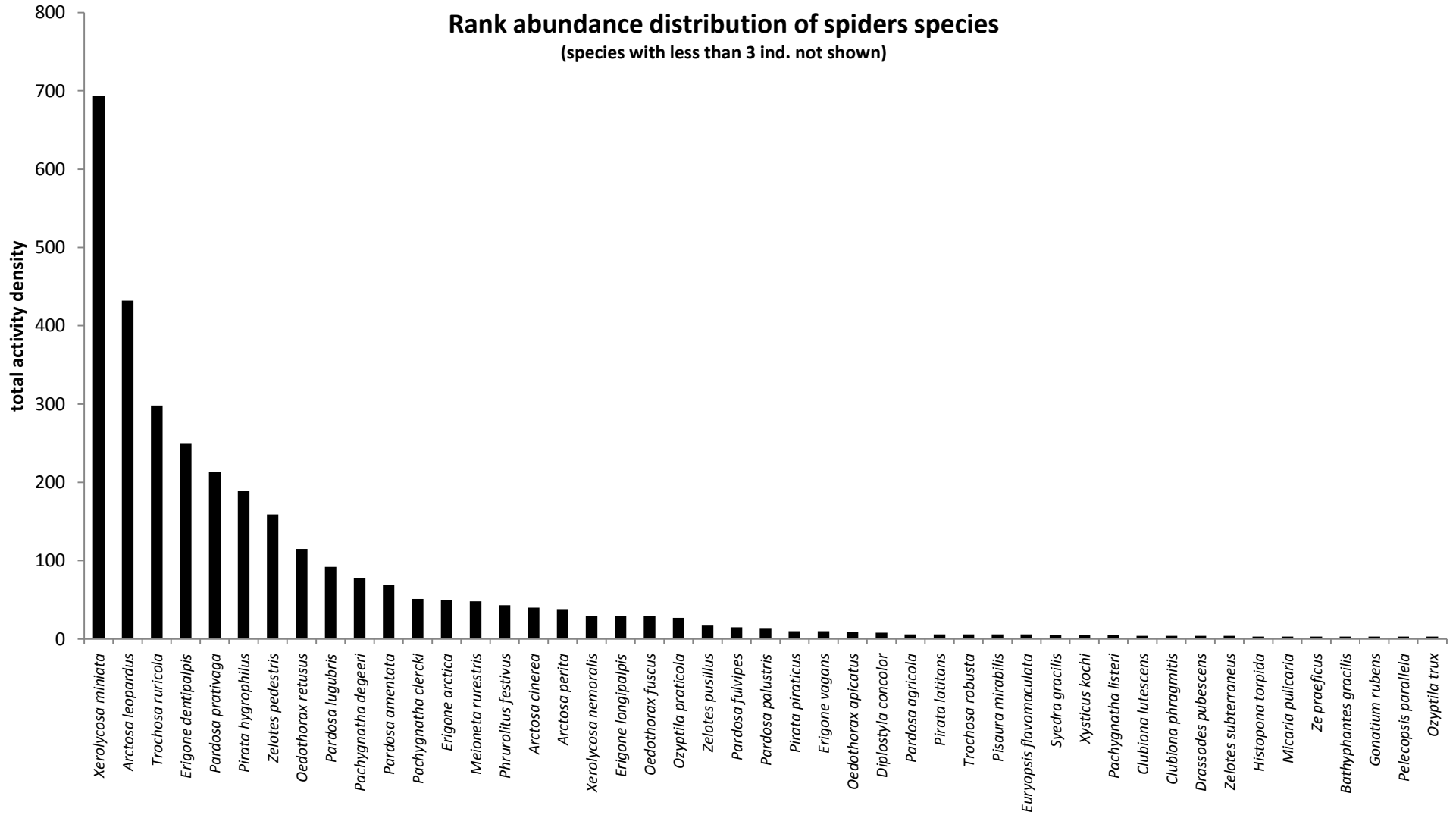


**Fig. 1** log-log diagrams of Abundance occupancy distributions for spiders (left) and ground beetles (right).



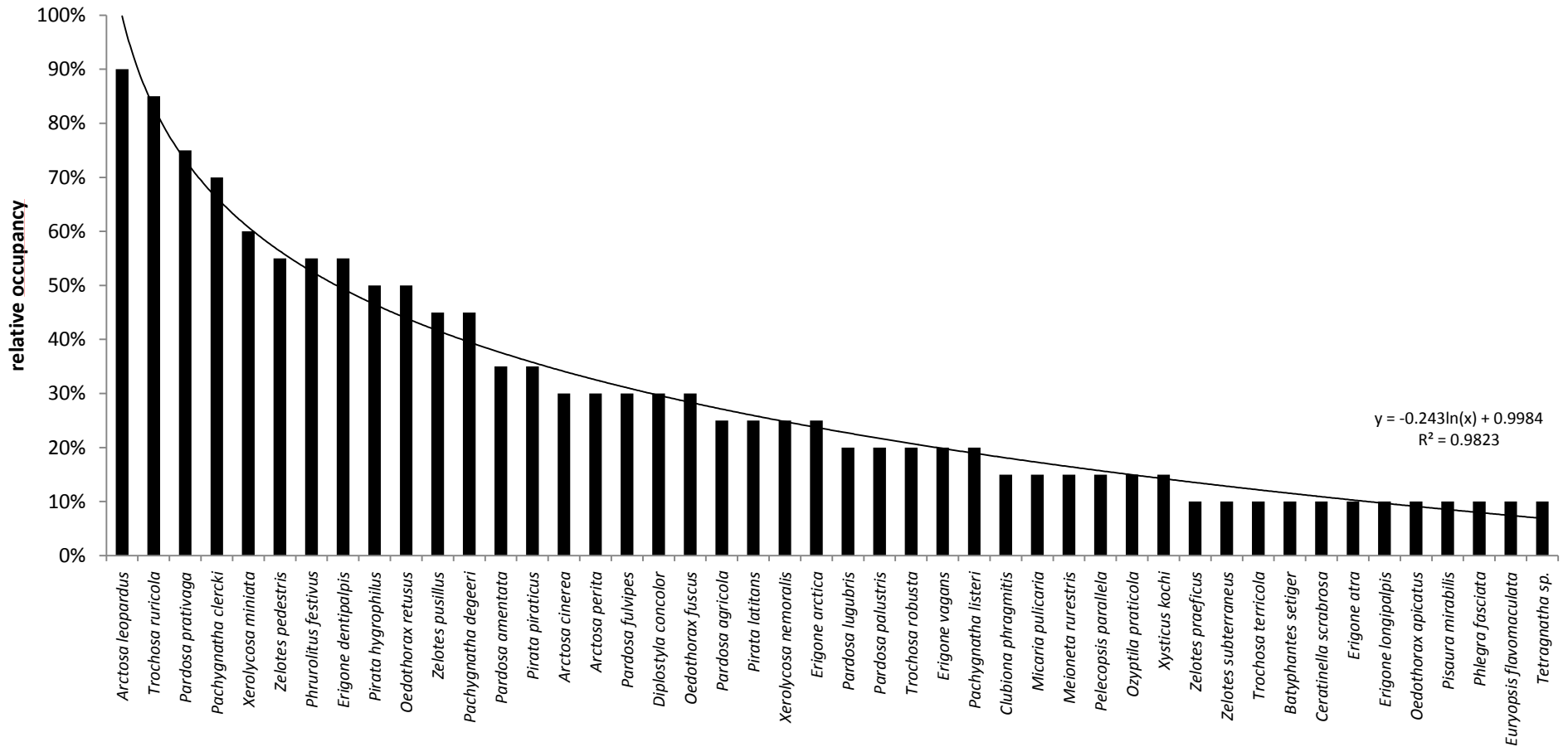


**Fig. 2** Rank Abundance Distribution of ground beetles with more than three individuals



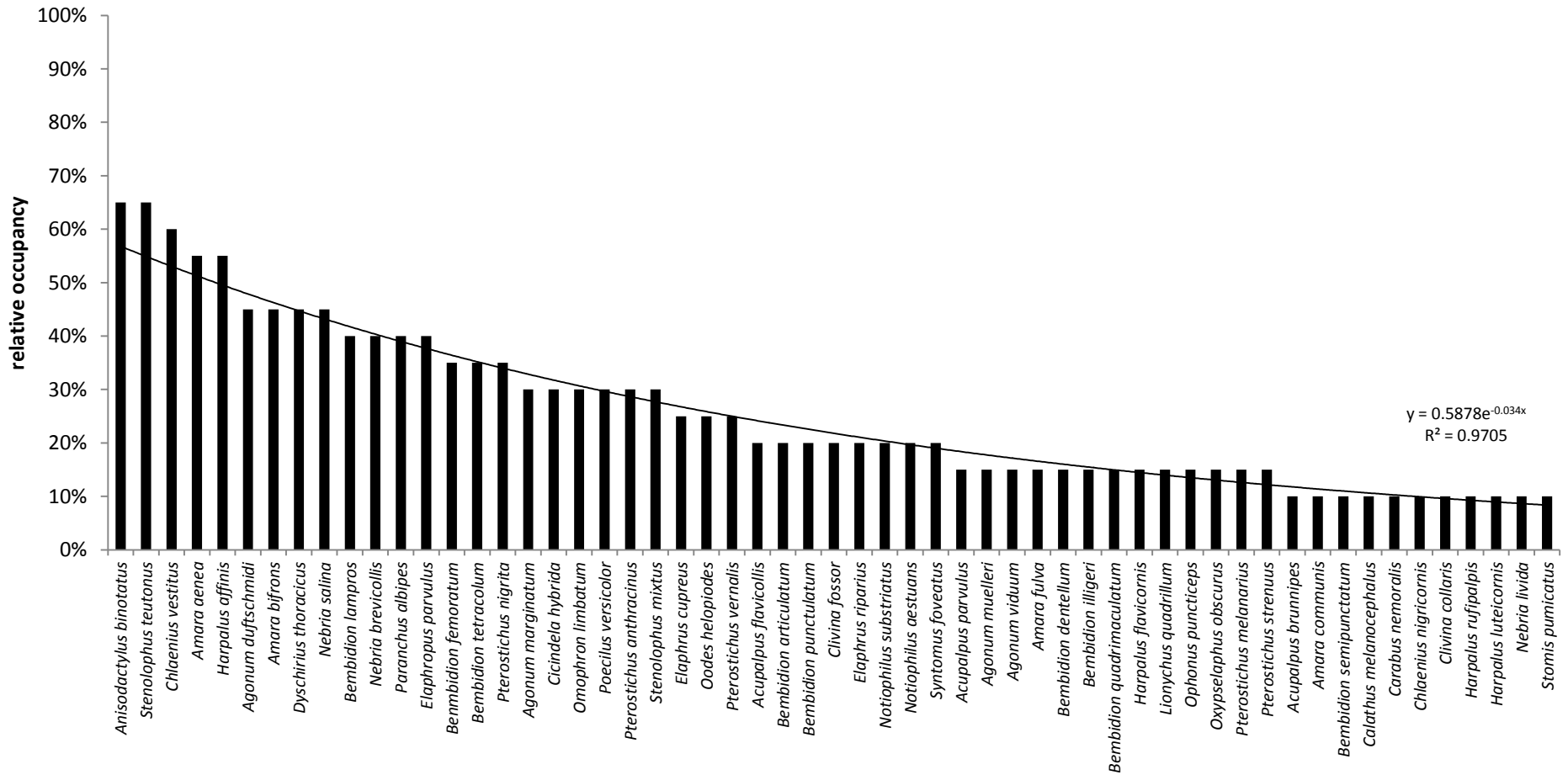
**Fig. 3** Rank Abundance Distribution for spiders with more than three individuals

**Ranked species occupancy curve of spider species**  
(species with occupancy < 10% not shown)



**Fig. 4** Ranked species occupancy curves for spiders with occupancies > 10%. On the y-axis relative occupancy is given as the proportion of all islands occupied by a species.

**Ranked species occupancy curves of ground beetle species**  
(species with occupancy < 10 % not shown)



**Fig. 5** Ranked species occupancy curves for ground beetles with occupancies > 10 %. On the y-axis relative occupancy is given as the proportion of all islands occupied by a species

### *Species area relationships*

Species numbers of spiders and ground beetles significantly increased with island area. The number of spider species increased with island area at a slightly steeper slope, compared to ground beetles and the proportion of variance explained by area was higher for spiders (Tab. 3). When Linyphiidae and other web-building spiders were excluded from the dataset and only true vagrant, ground-dwelling spiders were considered, the slope of the SAR became steeper, but the variance explained remained the same. While the species richness of Lycosidae alone was positively related to island area, the species richness of Linyphiidae showed no relation to island area at all (Fig 6; Tab 3)

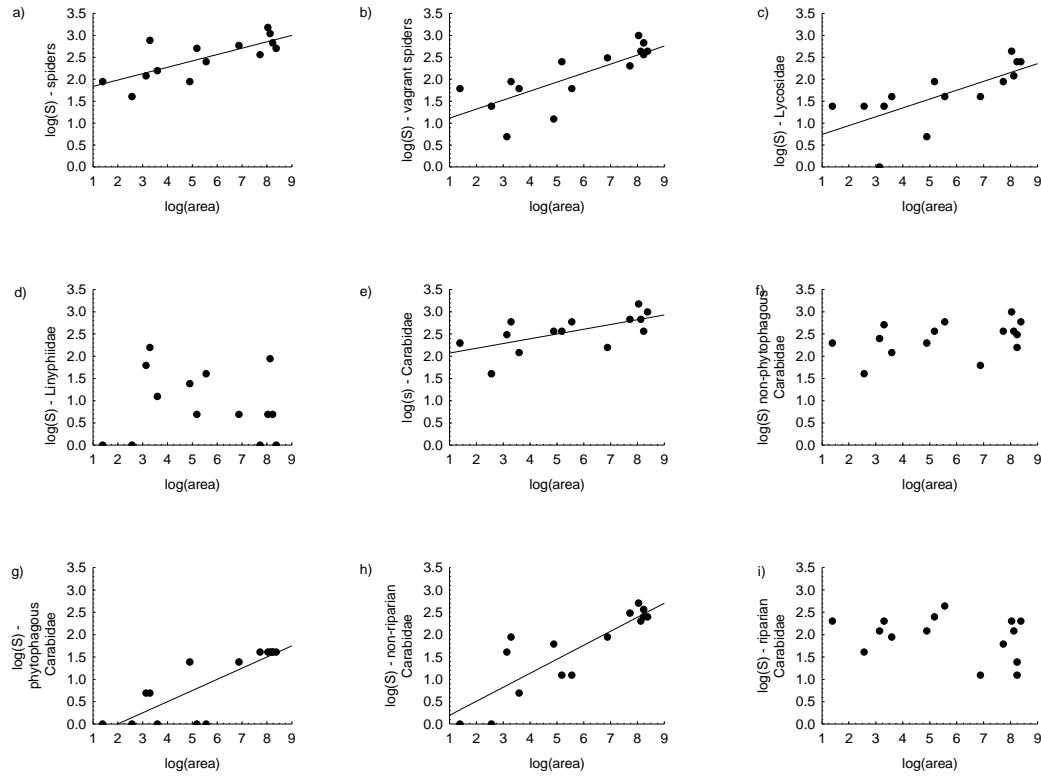
Ground beetle subgroups differed strongly in their response to area. When ground beetles were grouped by feeding type, phytophagous ground beetles showed a steep and significant increase with island area, while predacious ground beetles only showed a non-significant positive trend. When ground beetles were grouped as riparian and non-riparian species, the numbers of non-riparian ground beetle species strongly increased with area, while the number of riparian species showed a slightly negative but non-significant trend (Fig 6; Tab 3).

Spider densities, measured as catches per trap and subgroups of vagrant spiders and wolf spiders showed positive but non-significant trends of increase with island area. The density of Linyphiidae significantly decreased with island size when the newly created island (D10) was removed. The catches per trap of Linyphiidae on island D10 differed from catches on all other islands by an order of magnitude. The density (catches per trap) of ground beetles increased marginally significant with island area, densities of phytophagous and non-riparian subgroups significantly increased with island area, while densities of predacious and riparian subgroups did not (Fig. 7; Tab. 3).

Jackknife rarefaction added little changes to the species area relationships of both arthropod groups (See Tab. 3). Observed species numbers were at average 71.5 % ( $\pm 5.9\%$ ) of Jackknife estimates for ground beetles and 69.2 % ( $\pm 3.2\%$ ) for spiders (Tab. 4). Observed proportions of Jackknife estimates were unrelated to area in both groups ( $p > 0.05$ ; Pearson regression).

**Tab. 3:** Species-area (SAR) and density-area relationship (dAR) for spiders and carabids, S = total number of species and N = total number of individuals involved in the relationship; r = correlation coefficient; p = significance level (\* < 0.05, \*\* < 0.01, \*\*\* < 0.001, NS > 0.5)

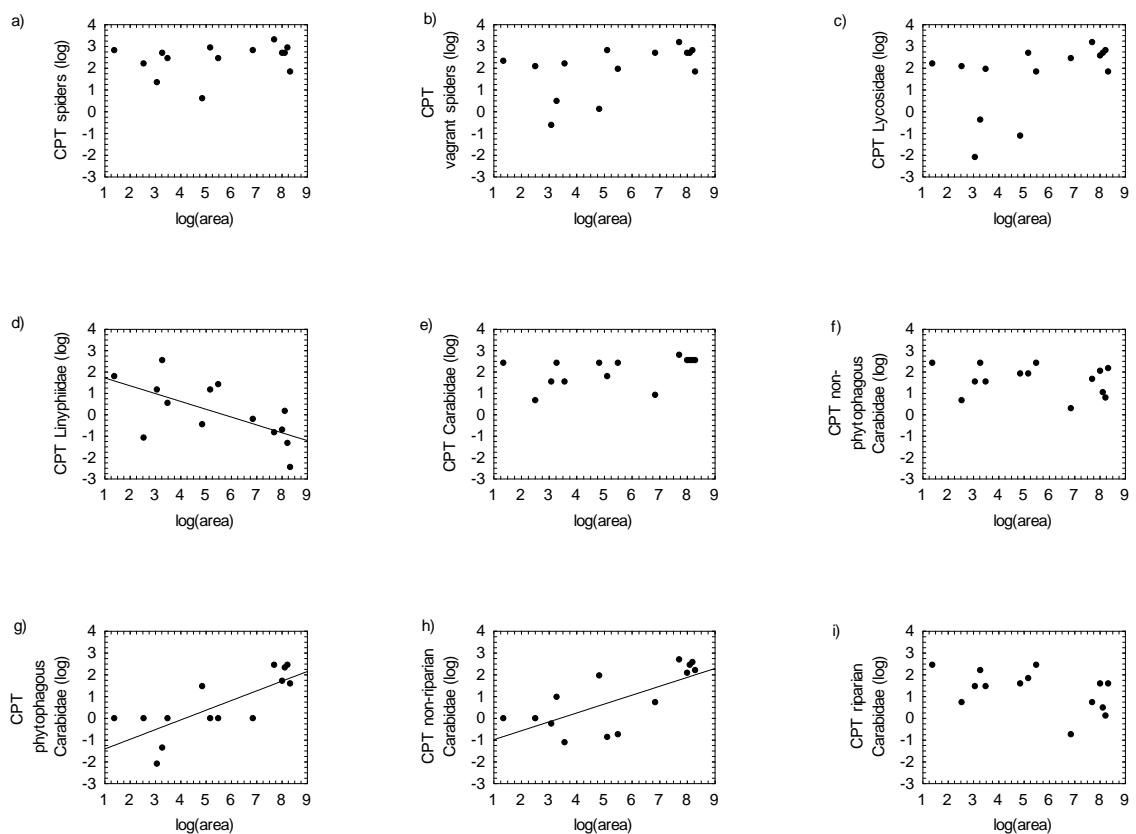
Group	S	I	SAR	dAR	r(SAR)	r(dAR)	p(SAR)	p(dAR)
<b>Spiders</b>	67	1969	$S=5.4A^{0.15}$	$I=4.0A^{0.08}$	0.75	0.36	**	< 0.1
<b>Spiders (Jackknife)</b>	---	---	$S=7.7A^{0.16}$	---	0.76	---	**	---
<b>Vagrant spiders</b>	53	1422	$S=2.5A^{0.21}$	$I=1.9A^{0.23}$	0.75	0.49	**	< 0.1
<b>Lycosidae</b>	24	1294	$S=1.7A^{0.20}$	$I=0.9A^{0.31}$	0.70	0.46	**	< 0.1
<b>Linyphiidae</b>	30	523	$S=3.0A^{0.03}$	$I=8.1A^{-0.36}$	-0.09	-0.64	NS	*
<b>Ground beetles</b>	63	1620	$S=7.1A^{0.12}$	$I=4.1A^{0.11}$	0.64	0.43	*	NS
<b>Ground beetles (Jackknife)</b>	---	---	$S=9.8A^{0.11}$	---	0.66	---	*	---
<b>Non-phytophagous Carabidae</b>	56	975	$S=7.9A^{0.06}$	$I=7.4A^{0.07}$	0.38	-0.25	NS	NS
<b>Phytophagous Carabidae</b>	7	645	$S=1.6A^{0.25}$	$I=0.2A^{0.45}$	0.82	0.77	***	**
<b>Riparian Carabidae</b>	36	693	$S=9.4A^{-0.04}$	$I=9.0A^{0.17}$	-0.23	-0.47	NS	< 0.1
<b>Non-riparian Carabidae</b>	27	927	$S=0.9A^{0.33}$	$I=0.2A^{0.41}$	0.85	0.72	***	**



**Fig. 6** Double-log species area relationships: a) All spiders; b) vagrant spiders; c) Lycosidae; d) Linyphiidae; e) all ground beetles, f) non-phytophagous ground beetles; g) phytophagous ground beetles; h) non-riparian ground beetles; i) riparian ground beetles

**Tab. 4:** Observed and estimated species richness on islands and mainland sites; S = species richness; GB = ground beetles

Island	S (GB)	S (spiders)	Jacknife (GB)	Jacknife (spiders)	Observed percent of estimate for GB	Observed percent of estimate for spiders	Island area (m <sup>2</sup> )
BF	14	11	19	15	73.7	73.3	---
DF	22	22	28	31	78.6	71.0	---
DS	27	25	42	35	64.3	71.4	---
DW	21	31	28	47	75.0	66.0	---
B1	10	7	14	9	71.4	77.8	4
B11B	5	5	8	8	62.5	62.5	13
D1	12	8	17	12	70.6	66.7	23
D2	16	18	24	27	66.7	66.7	27
B11A	8	9	11	13	72.7	69.2	36
D3	13	7	16	10	81.3	70.0	133
B8	13	15	16	21	81.3	71.4	177
B12	16	11	21	15	76.2	73.3	258
B2	9	16	13	24	69.2	66.7	970
D10	27	23	34	34	79.4	67.6	1850
D4	17	13	24	19	70.8	68.4	2263
D6	24	24	38	35	63.2	68.6	3096
D8	17	21	25	32	68.0	65.6	3375
D5	13	17	19	23	68.4	73.9	3763
D7	20	15	30	23	66.7	65.2	4340



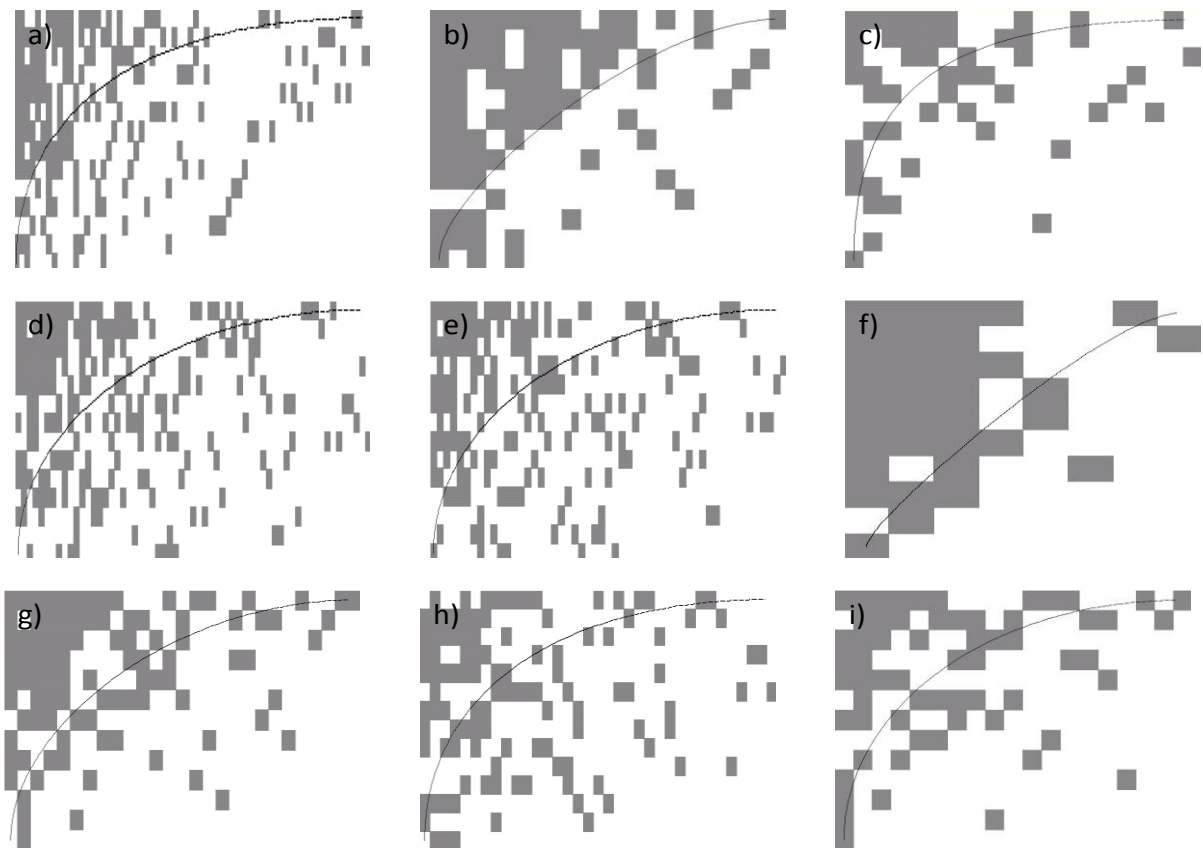
**Fig. 7** Double-log density area relationships with area on the x-axis and catches per trap on the y-axis: a) all spiders; b) vagrant spiders; c) Lycosidae; d) Linyphiidae; e) all ground beetles; f) non-phytophagous ground beetles; g) phytophagous ground beetles; h) non-riparian ground beetles; i) riparian ground beetle

### *Nestedness*

All groups and subgroups of arthropods were significantly nested. However, nestedness temperatures showed substantial variation (Fig. 8; Tab. 5). The lowest nested temperatures were calculated for phytophagous ground beetle species and non-riparian, non-wetland ground beetles.

I report the following analogy without statistical testing, because species lists in subgroups partially overlapped, causing spurious correlations:

Nestedness temperatures of all arthropod groups were negatively correlated to the slopes ( $z$ ) of SARs ( $r = -0.84$ ) when Linyphiids were omitted from the analysis (Linyphiidae had no slope ( $z$ )), i.e. the degree of nestedness increased with the steepness of the species area relationship.



**Fig. 8** Nestedness plots of spiders and ground beetles with species on the x-axis and sampling sites on the y-axis; a grey block denotes a species occurrence; note that differences in species richness and site occupancy between animal groups lead to differences in matrix size: a) all spiders b) Lycosidae c) Linyphiidae d)all ground beetles e) non-phytophagous ground beetles; f) phytophagous ground beetles; g) non-riparian ground beetles h) riparian ground beetles i) non-riparian, non-phytophagous ground beetles

**Tab.5:** Nestedness temperatures after Atmar & Petterson (1998),  $T_{null}$  = Mean nestedness temperature of 1000 randomized matrices,  $T$  = nestedness temperature of actual community,  $SD$  = standard deviation;  $P$  = significance level (\* < 0.05, \*\* < 0.01, \*\*\* < 0.001, NS > 0.5)

Group	$T_{null}$	Matrix fill	SD	$T$	$P(T = T_{null})$
<b>Spiders</b>	50.33°	21.4 %	± 4.36°	30.77°	***
<b>Ground beetles</b>	55.47°	24.8 %	± 4.66°	41.60°	**
<b>Lycosidae</b>	52.28°	34.0 %	± 7.06°	21.47°	***
<b>Linyphiidae</b>	36.85°	19.5 %	± 7.23°	20.20°	*
<b>Non- phytophagous ground beetles</b>	52.54°	24.1 %	± 4.77°	41.41°	**
<b>Phytophagous ground beetles</b>	41.46°	41.2 %	± 10.40°	13.85°	**
<b>Riparian ground beetles</b>	49.03°	23.0 %	± 5.89°	36.12°	*
<b>Non-Riparian ground beetles</b>	50.88°	27.3 %	± 6.45°	16.00°	***
<b>Non-riparian - non -phytophagous</b>	45.16°	25.5 %	± 7.91°	17.13°	***



### Similarity

An analysis of similarity (ANOSIM) revealed that the Jaccard dissimilarity between island groups of the Brüggelhofsee and the Diersfordter Waldsee was significantly higher than between islands within each lake for spiders and carabids (Tab. 6).

**Tab. 6:** Results of ANOSIM, testing for dissimilarities between the community composition of Brüggelhofsee and Diersfordter Waldsee (Jaccard distance).  $r_w$  = mean rank within groups;  $r_b$  = mean rank between groups;  $p$  = significance level = probability that communities are perfectly similar; i.e. significance denotes a 95 % probability of community dissimilarity (\* < 0.05, \*\* < 0.01, \*\*\* < 0.001, NS > 0.5)

Arthropod group	$r_w$	$r_b$	R	significance (p)
<b>Ground beetles</b>	71.9	121.2	0.52	***
<b>Spiders</b>	86.4	105.4	0.20	*

### Co-occurrence

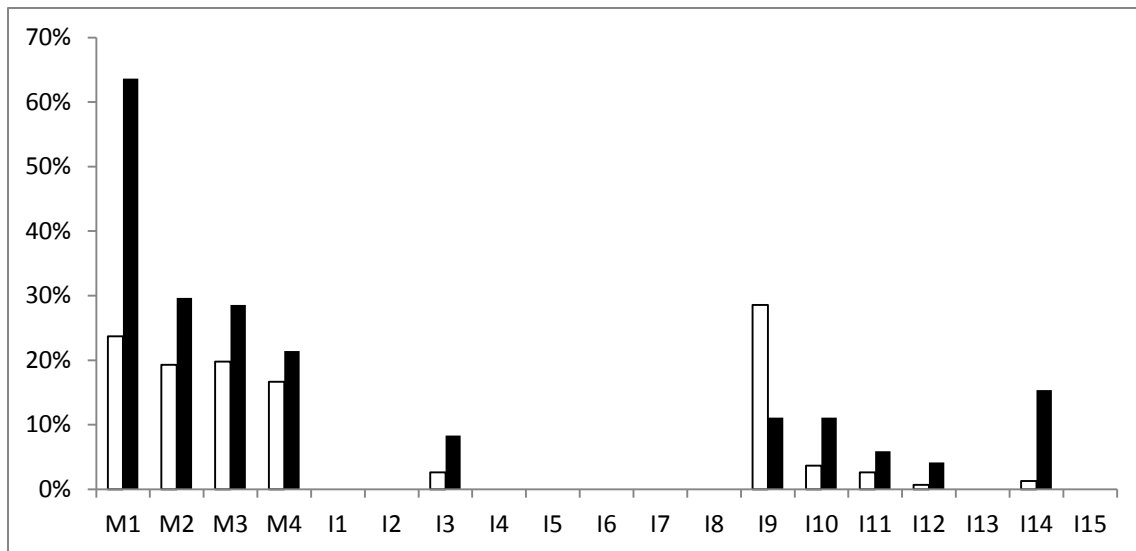
Co-occurrence analysis revealed C-Scores, which were significantly higher than expected by chance for ground beetles and spiders within the system of the Diersfordter Waldsee. For ground beetles also the Checkerboard score was significantly higher than expected by chance (Tab. 7).

**Tab. 7:** C-scores and Checkerboard score for spiders and ground beetles;  $p$  = significance level

Arthropod group	Score	Observed index	Mean of sim Indices	Variance of sim indices	$p$ (observed $\geq$ expected)
<b>Spiders</b>	C-Score (SS)	3.914	3.801	0.00161	0.0052
<b>Ground beetles</b>	C-Score (SS)	3.747	3.491	0.00070	< 0.0001
<b>Ground beetes</b>	Checkerboard	1241	1210	240	0.0378

### Between island distribution of ground beetle species according to hind wing development

The fractions of brachypterous ground beetle species and individuals were generally higher on mainland sites ( $N = 4$ ) than on islands ( $N = 15$ ) (MWU-Test;  $p < 0.01$ ). In fact, the majority of island communities contained no brachypterous individuals at all (Fig. 9). Some of the brachypterous individuals on larger islands were members of dimorphic species. Members of dimorphic species on small islands were all macropterous with the single exception of a brachypterous individual of *Bembidion tetracolum* (Say, 1823) on an island sized 25 m<sup>2</sup>. The fractions of brachypterous species or individuals were not related to island area in a linear fashion (Pearsson regression;  $r = 0.19$ ;  $p = 0.5$ ). When islands were grouped into categories of small ( $N = 8$ ) and large islands ( $N = 7$ ), brachypterous species occurred significantly more frequent on large islands (MWU-test;  $p < 0.05$ ). However, the number of brachypterous individuals was not significantly, but only marginally higher on large islands ( $p = 0.06$ ). Most of the brachypterous species on islands were rare. Noteworthy, individuals of the species *Syntomus foveatus* (Geoffroy, 1785) were brachypterous on the mainland site it occurred at, while on a small island they were macropterous; according to the literature macropterous *Syntomus foveatus* are rarely observed.

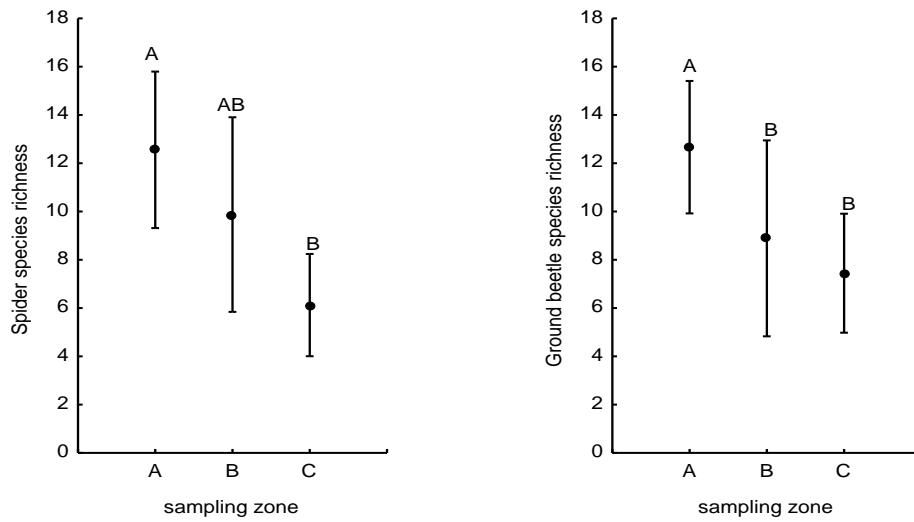


**Fig. 9** Fraction of brachypterous ground beetle species (black bars) and individuals (white bars) on mainland sites (M#) and islands (I#).

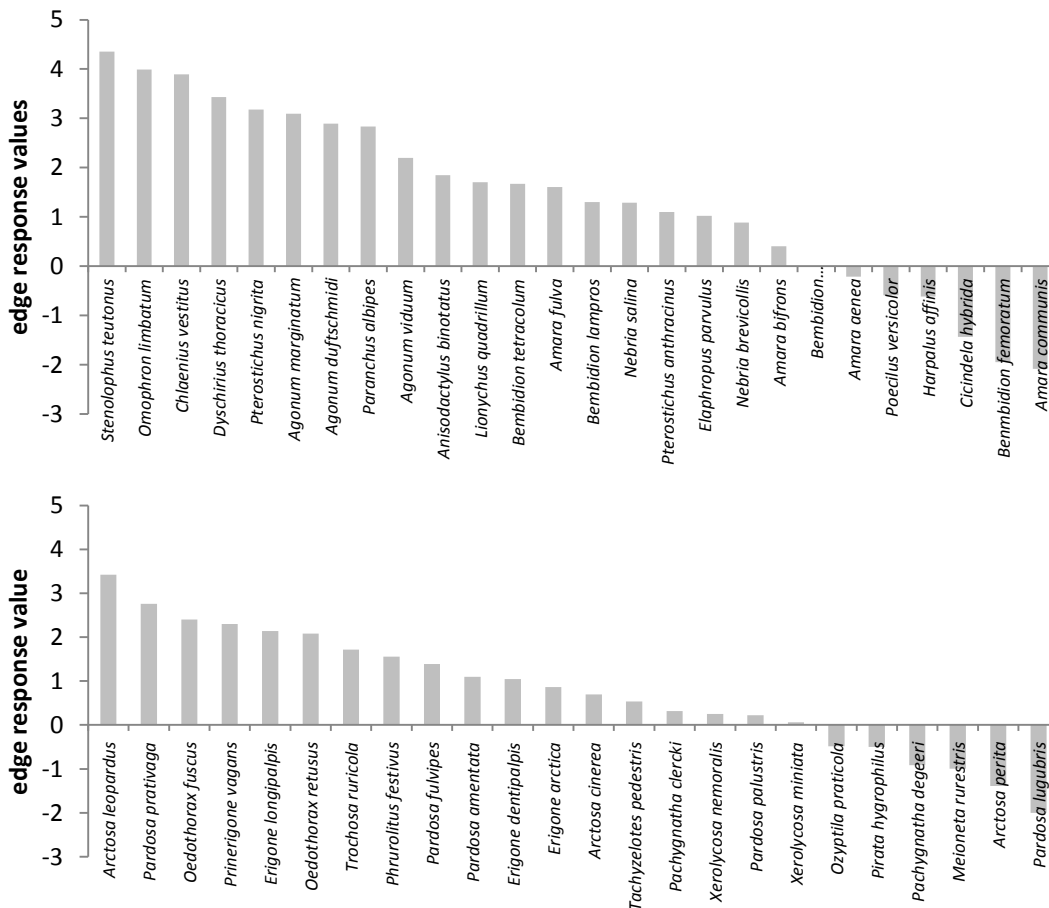
#### *Within-islands species distribution*

On the larger islands, species richness of ground beetles and spiders increased rather gradually towards the shore with statistical significance (one-way ANOVA; spiders:  $p < 0.05$ ; ground beetles:  $p < 0.05$ ). However, due to a spillover of the most abundant ground beetle species *A. aenea* and the wolf spider *X. miniata* from dry habitats in islands centers into the shore zones, there were no differences in catches per trap between the three zones (one-way ANOVA; spiders:  $p = 0.11$ ; ground beetles:  $p = 0.75$ ).

Edge response values of locally common ground beetle species reached higher maxima than locally common spider species but were not generally higher (one-way ANOVA). The distribution of positive and negative edge response values was remarkably similar for ground beetles and spiders. The majority of spider species (18 species) and ground beetles (19 species) had positive edge response values, while in both groups only six showed negative edge response values. The two most active and common species *A. aenea* and *X. miniata* had near neutral distributions (edge response values near zero), i.e. they both peaked in the B zone (2,80 m distance from the shoreline)(Fig. 11). The logit of species occurrence increased with edge response for spiders (Pearsson regression;  $r = 0.52$ ;  $r^2 = 0.27$ ;  $p < 0.01$ ) and ground beetles ( $r = 0.32$ ;  $r^2 = 0.10$ ;  $p = 0.11$ ).



**Fig. 10** Differences in mean species richness between island sampling zones for spiders (left) and ground beetles (right); island shore (Zone A); 2,8 m inland (Zone B); island center (Zone C); bars denote 95 % confidence interval; different letters above bars denote a significant difference.



**Fig. 11** Edge response values for ground beetles (upper) and spiders (lower) with more than 10 individuals

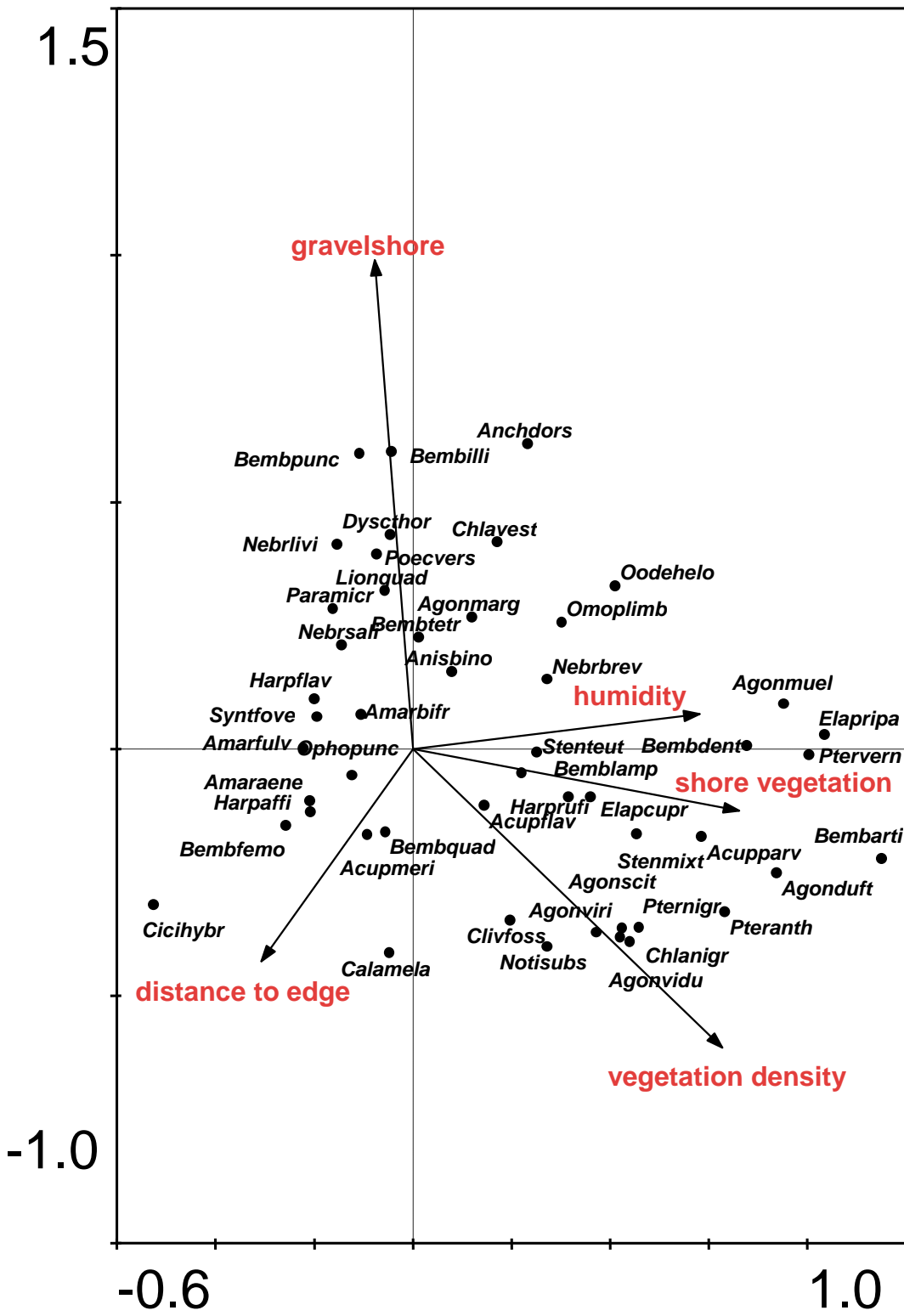
## Relationships between species and their environment

### *Explorative methods - Canonical Correspondence Analysis*

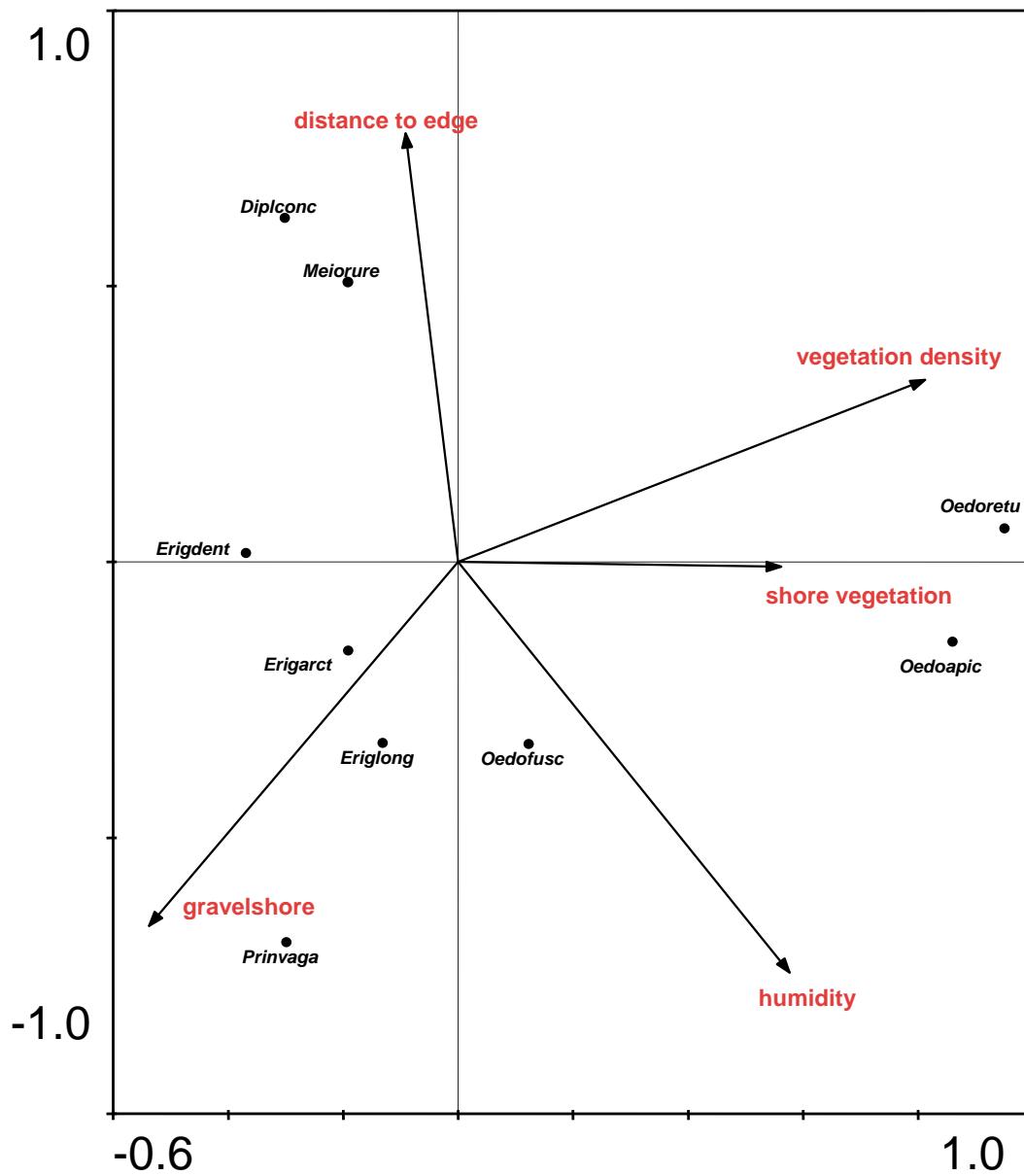
In the CCA two axes explained 74.3 % of the variance of the species-environment relations for ground beetles, 83.9 % for vagrant spiders and 81.5 % of the variance for Linyphiidae (Tab. 9). For ground beetles, 49.2 % of the variance was explained by vegetation density and humidity, while another ~25 % was explained by the gravel type shore alone (Fig. 12). For vagrant spiders 83.9 % of the variance was explained by vegetation density and shore vegetation (Fig. 13), while for Linyphiidae, vegetation density, humidity and distance to shore were the most important environmental factors (Fig 14). All models were significant (1000 Monte-Carlo runs).

**Tab. 10:** Results for the Canonical Correspondence Analysis for ground beetles, vagrant spiders and Linyphiidae.

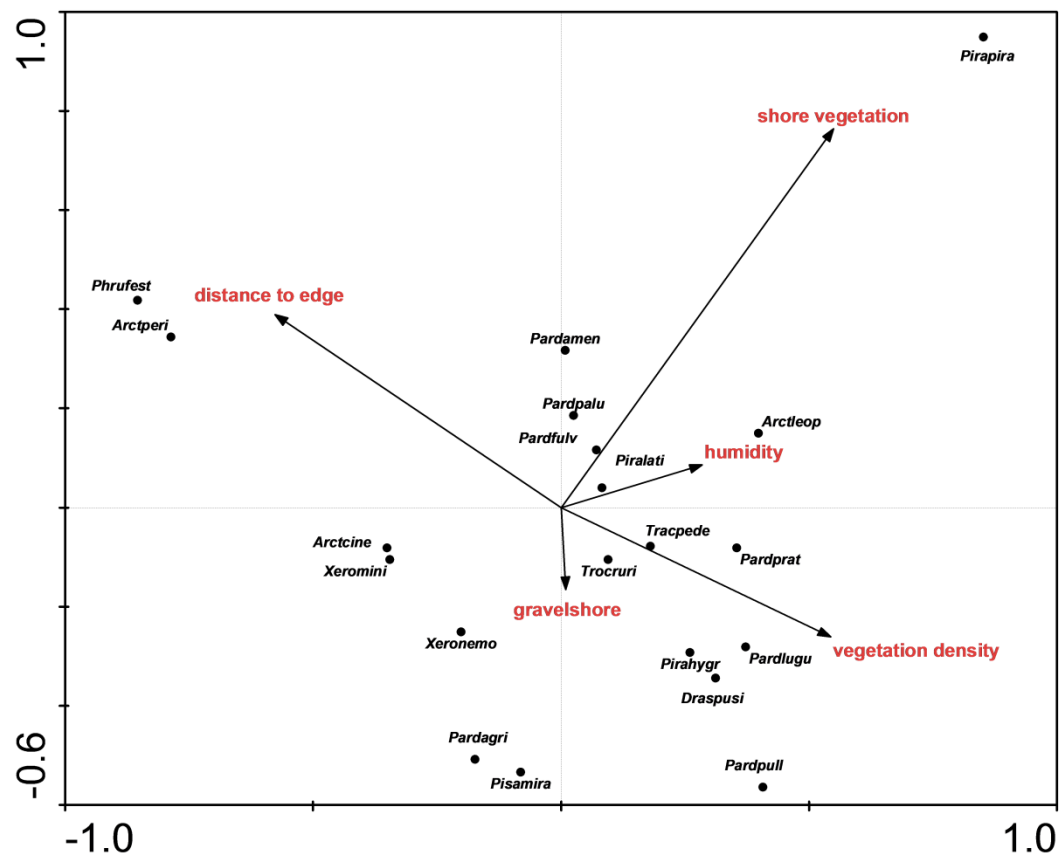
CCA for ground beetles	Axis 1	Axis 2	Axis 3	Axis 4	Total inertia
<b>Eigenvalues</b>	0.378	0.193	0.099	0.055	7.837
<b>Species - Environment correlations</b>	0.734	0.677	0.611	0.450	----
<b>Explained variance species data</b>	4.8	7.3	8.5	9.2	----
<b>Species environment relation</b>	49.2	74.3	87.1	94.3	----
CCA for vagrant spiders					
<b>Eigenvalues</b>	0.323	0.094	0.062	0.012	3.945
<b>Species -Environment correlations</b>	0.728	0.559	0.522	0.260	----
<b>Explained variance species data</b>	8.2	10.6	12.1	12.4	----
<b>Species environment relation</b>	65.0	83.9	96.4	98.9	----
CCA for Linyphiidae					
<b>Eigenvalues</b>	0.445	0.128	0.088	0.033	2.713
<b>Species -Environment correlations</b>	0.763	0.628	0.529	0.323	----
<b>Explained variance species data</b>	16.4	21.1	24.4	25.6	----
<b>Species environment relation</b>	63.3	81.5	94.0	98.7	----



**Fig. 12** CCA of ground beetles in relation to their environment; species abbreviations given in the Appendix



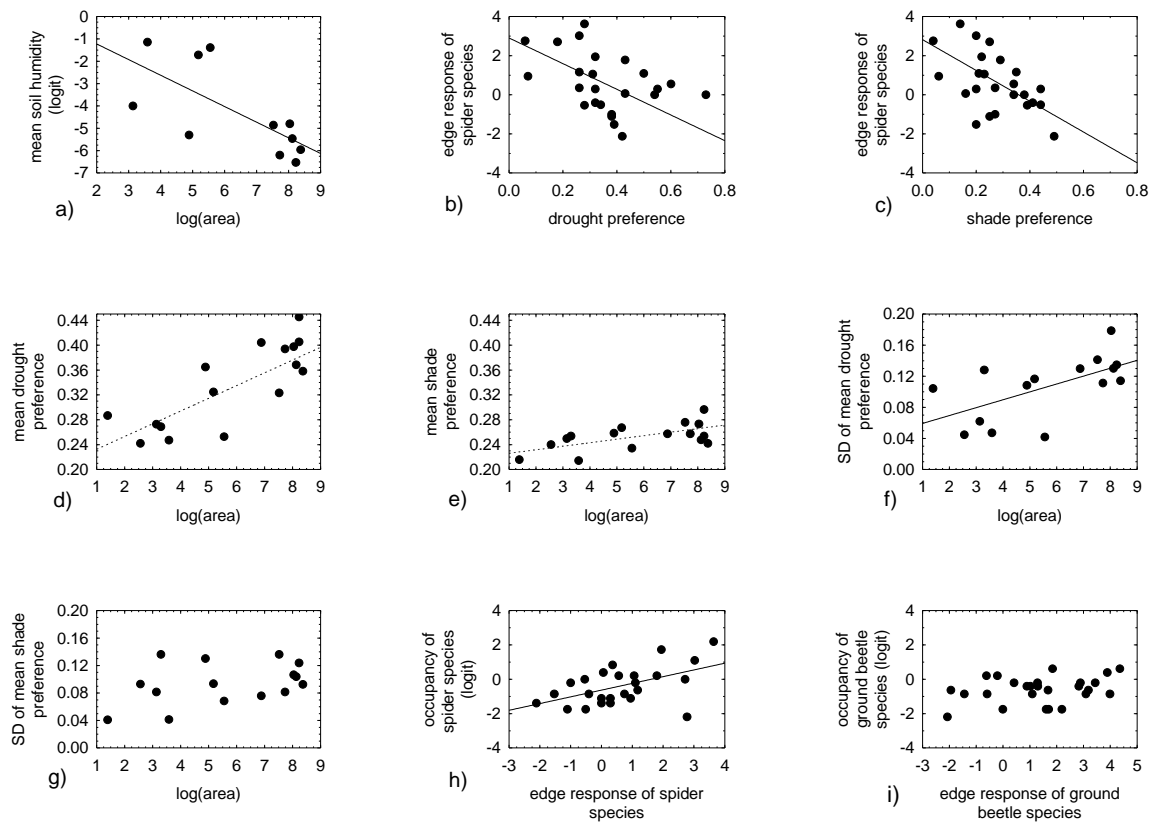
**Fig. 13** CCA of Linyphiidae in relation to their environment; species abbreviations given in the Appendix



**Fig. 14** CCA of vagrant spiders in relation to their environment; species abbreviations given in the Appendix

*Niche distribution in spiders*

Values of shade and drought preference were significantly related to edge response values in spiders. Furthermore mean drought preference values and the standard deviation of mean drought preference values for spiders increased with island area. Mean shade preference values also increased with island area, but the standard deviation of shade preference values did not (Fig. 15; Tab. 11).



**Fig.15** Correlation of a) logit of soil humidity with island size, b) correlation of edge response of spiders with drought preference and c) with shade preference, d) correlation of drought preferences and log-island area e) of shade preference with log-island area, f) standard deviation of mean drought preference of spiders and g) standard deviation of mean shade preference of spiders with (log) island area, and h) correlation of occupancy and edge response of spider species and i) correlation of occupancy and edge response of beetle species on larger islands with three sampling zones applied; SD = standard deviation



**Tab. 11:** Results of regressions and correlations in Fig. 15

Regression / Correlation	r	r <sup>2</sup>	p - level
Logit mean soil humidity - log area	-0.70	0.48	*
Spiders edge response - drought preference	-0.49	0.24	*
Spiders edge response - shade preference	-0.55	0.30	*
Mean drought preference – log area	0.80	0.63	***
Mean shade preference – log area	0.62	0.38	*
STD drought preference - log area	0.61	0.37	*
STD shade preference - log area	0.40	0.16	NS
Spider occupancy - edge response	0.52	0.27	**
Carabidae occupancy - edge response	0.31	0.10	NS

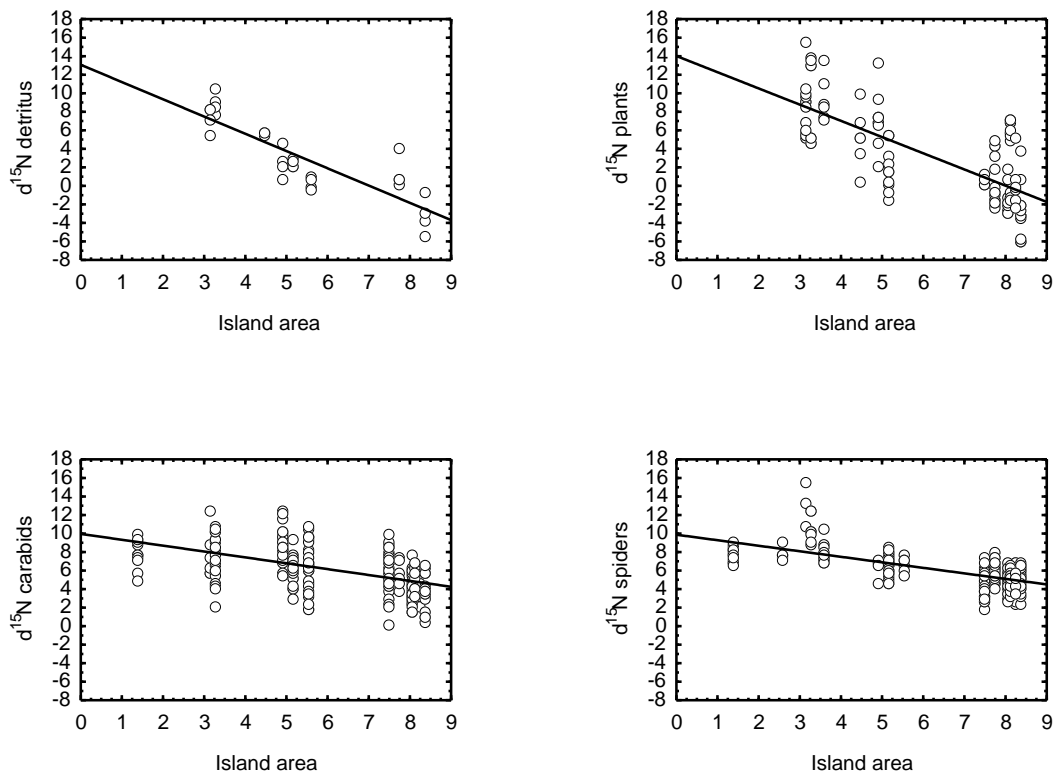
### *Stable isotope results*

Of the 1450 samples prepared and analyzed, 1429 yielded results without reported problems. Three samples of the large rove beetle *Ocypus olens* (Müller, 1764) had to be discarded due to problems during the automated analysis. For another 18 samples the precision of reported isotopic signatures was reduced, because of nitrogen contents below 20 µg or carbon contents below 100 µg in the samples. Reduced precisions were reported for samples from plants, algae and bird feces. Ground beetles had lower mean values, but a wider range between maxima and minima and higher standard deviations for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures than spiders. Plants and detritus had very similar means and ranges of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures, but plants had higher maximum  $\delta^{15}\text{N}$  signatures. Bird feces showed the most extreme variation in  $\delta^{13}\text{C}$  signatures, while minimum and maximum  $\delta^{15}\text{N}$  signatures were similar to terrestrial plants, although mean  $\delta^{15}\text{N}$  signatures were generally higher than the mean  $\delta^{15}\text{N}$  signatures of arthropod predators like spiders and ground beetles (Tab. 12). On small bird islands, ground beetles and spiders, but also flies and springtails showed extremely high  $\delta^{15}\text{N}$  signatures.

**Tab. 12:** Descriptive statistics for groups of stable isotope samples; SD = standard deviations

Group	N	Mean $\delta^{13}\text{C}$	Min. $\delta^{13}\text{C}$	Max. $\delta^{13}\text{C}$	SD $\delta^{13}\text{C}$	Mean $\delta^{15}\text{N}$	Min. $\delta^{15}\text{N}$	Max. $\delta^{15}\text{N}$	SD $\delta^{15}\text{N}$
spiders	266	-26.81	-28.91	-23.11	0.97	6.12	-0.41	16.82	2.24
carabidae	312	-27.65	-30.66	-22.07	1.29	5.50	-1.28	16.90	3.08
plant	119	-29.15	-32.39	-25.70	1.20	3.09	-6.14	15.55	5.00
detritus	32	-29.24	-31.08	-22.92	1.46	3.14	-5.50	10.51	3.92
feces	15	-22.91	-29.05	-13.13	6.22	8.97	6.43	15.14	2.60

In the analyzed dataset,  $\delta^{13}\text{C}$  signatures were significantly related to  $\delta^{15}\text{N}$  signatures in ground beetles ( $r = 0.13$ ;  $p < 0.001$ ) and spiders ( $r = 0.47$ ;  $p < 0.001$ ). However, a more detailed analysis revealed species specific relationships between  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . In most ground beetle and spider species,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were unrelated to each other, e.g. in *Omophron limbatum* (Fabricius 1777) ( $r = 0.27$ ;  $p = 0.16$ ), *S. teutonius* ( $r = 0.15$ ;  $p = 0.4$ ), *C. vestitus* ( $r = 0.25$ ;  $p = 0.29$ ), *A. leopardus* ( $r = 0.14$ ;  $p = 0.26$ ), *P. prativaga* ( $r = 0.16$ ;  $p = 0.47$ ) and *Pachygnatha clercki* (Sundevall, 1823) ( $r = 0.29$ ;  $p = 0.21$ ). In some other species there was a clear positive relationship, like in the wolf spiders *T. ruricola* ( $r = 0.47$ ;  $p < 0.01$ ), *X. miniata* ( $r = 0.38$ ;  $p < 0.05$ ) and *A. cinerea* (Fabricius, 1777) ( $r = 0.52$ ;  $p < 0.05$ ). The two phytophagous ground beetle species *A. aenea* and *H. affinis* showed opposite relationships of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures. While in *A. aenea*, a clear positive relationship of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  was found ( $r = 0.57$ ;  $p < 0.001$ ), *H. affinis* showed a clear negative relationship of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ( $r = -0.71$ ;  $p < 0.001$ ). Very strong positive relationships of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were found in the two dwarf spider species *E. dentipalpis* ( $r = 0.85$ ;  $p < 0.001$ ) and *Oedothorax retusus* (Westring, 1851) ( $r = 0.93$ ;  $p < 0.001$ ). The  $\delta^{15}\text{N}$  signatures significantly decreased with island area in spiders ( $r = -0.67$ ;  $r^2 = 0.46$ ;  $p < 0.001$ ), ground beetles ( $r = -0.57$ ;  $r^2 = 0.32$ ;  $p < 0.001$ ), plants ( $r = -0.72$ ;  $r^2 = 0.52$ ;  $p < 0.001$ ) and detritus ( $r = -0.71$ ;  $r^2 = 0.51$ ;  $p < 0.001$ ) (Fig. 16). This relationship held also when bird islands were removed. The decrease of  $\delta^{15}\text{N}$  signatures with island area was also visible at the level of species, which occurred across some size range of the islands, e.g. *A. leopardus* ( $r = -0.63$ ;  $r^2 = 0.4$ ;  $p < 0.001$ ) and *P. prativaga* ( $r = -0.79$ ;  $r^2 = 0.78$ ;  $p < 0.001$ ). These negative relationships between  $\delta^{15}\text{N}$  and island area differed in slopes between animals and plants/detritus (Fig. 16).

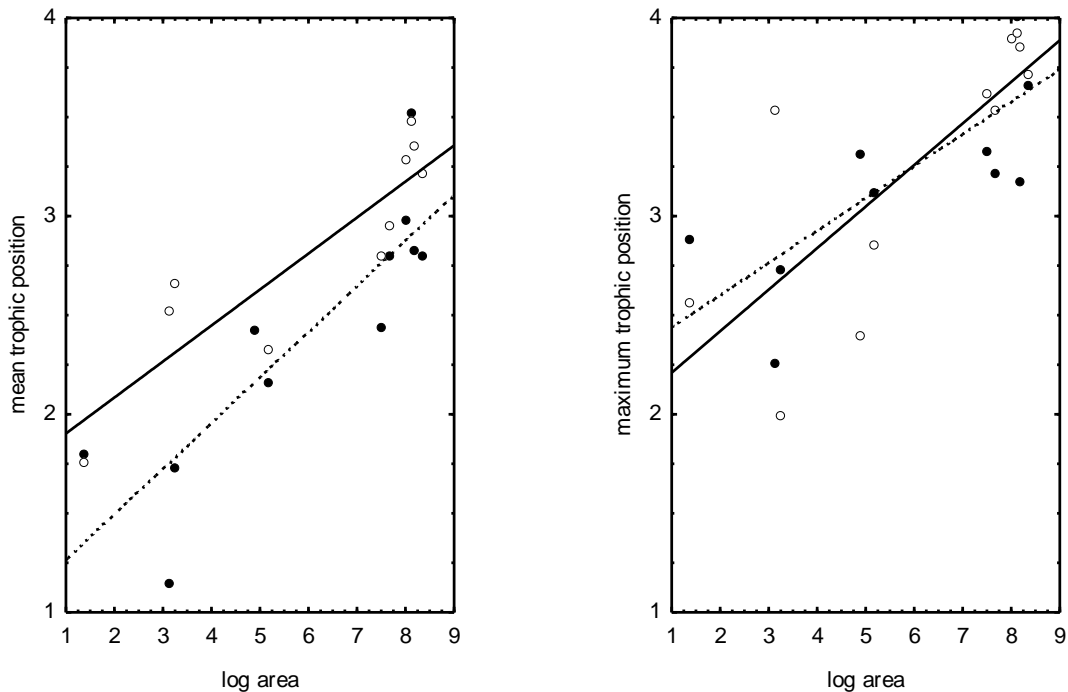


**Fig. 16** Correlations of  $\delta^{15}\text{N}$  with island area (log) for detritus (upper right), plants (upper left), ground beetles (lower left) and spiders (lower right)

Mean  $\delta^{15}\text{N}$  signatures slightly increased with edge response values of spiders ( $r = 0.21$ ;  $p < 0.001$ ) and ground beetles ( $r = 0.25$ ;  $p < 0.001$ ). Variation of  $\delta^{13}\text{C}$  signatures (SD) ( $r = 0.38$ ;  $p < 0.05$ ) also increased with edge response in spiders, but not in ground beetles ( $r = -0.17$ ;  $p = 0.26$ ).

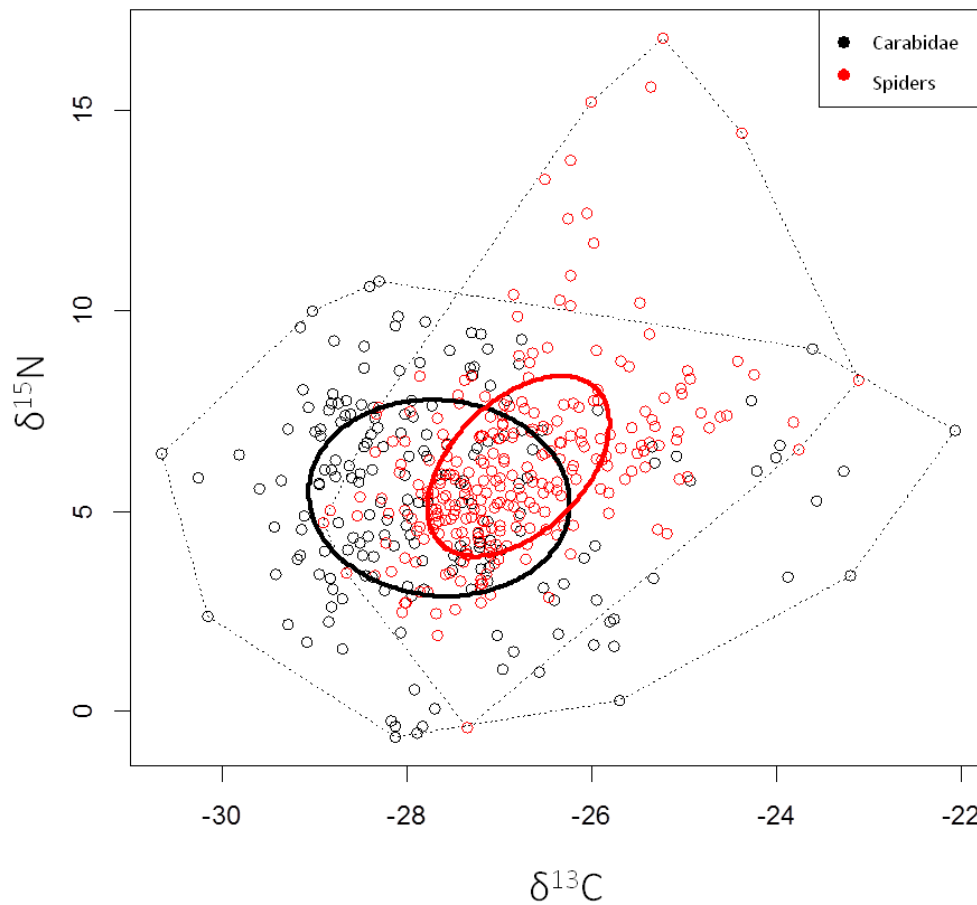
### *Food chain length*

Both proxy variables for food-chain length, mean trophic position and maximum trophic position were positively correlated to island area (Fig. 17).  $\delta^{15}\text{N}$  plant-baseline variation was high on most islands, with values of  $\delta^{15}\text{N}$  standard deviation (SD) typically exceeding 2.5 ‰.  $\delta^{15}\text{N}$  detritus-baseline variation (SD) was lower than  $\delta^{15}\text{N}$  plant-baseline variation and the  $\delta^{15}\text{N}$  SD of detritus increased with area.  $\delta^{15}\text{N}$  SD of herbivore-baseline ( $\sim 1.5$  ‰) was also lower than  $\delta^{15}\text{N}$  SD plant-baseline variation.  $\delta^{15}\text{N}$  SD of predatory ground beetles and spiders was not different from  $\delta^{15}\text{N}$  SD of herbivores.

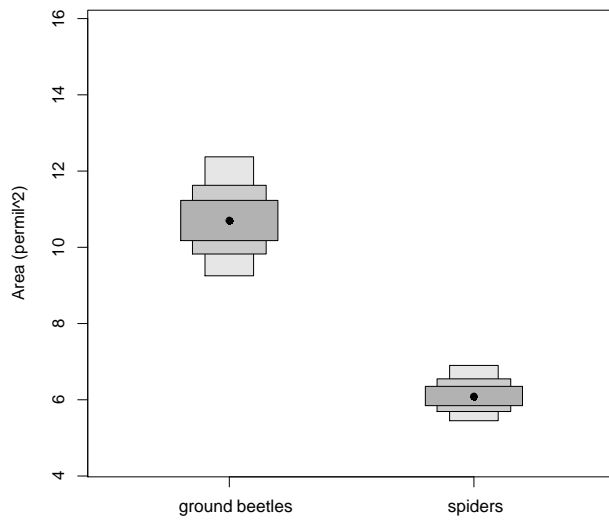


**Fig. 17** Food-chain area relationship for spiders (open circles; solid line; mean trophic position:  $r = 0.89$ ,  $r^2 = 0.79$ ,  $p < 0.001$ ; maximum trophic position:  $r = 0.77$ ;  $r^2 = 0.60$ ;  $p < 0.01$ ) and ground beetles (closed circles; dashed line; mean trophic position:  $r = 0.86$ ;  $r^2 = 0.74$ ;  $p < 0.001$ ; maximum trophic position:  $r = 0.75$ ;  $r^2 = 0.56$ ;  $p > 0.01$ )

Niche width, measured as corrected standard ellipse area ( $SEA_c$ ) and convex hull area (TA) of isotopic space was larger for ground beetles ( $SEA_c = 10.9$ ;  $TA = 65.6$ ) than for spiders ( $SEA_c = 6.1$ ;  $TA = 51.2$ )(Fig.19) with phytophagous ground beetles excluded from the dataset. 65.7 % of  $SEA_c$  (4.0) and 67 % of the TA (34.3) of spiders overlapped with that of ground beetles. Differences in  $SEA_c$  were significant in both cases (Fig. 18).



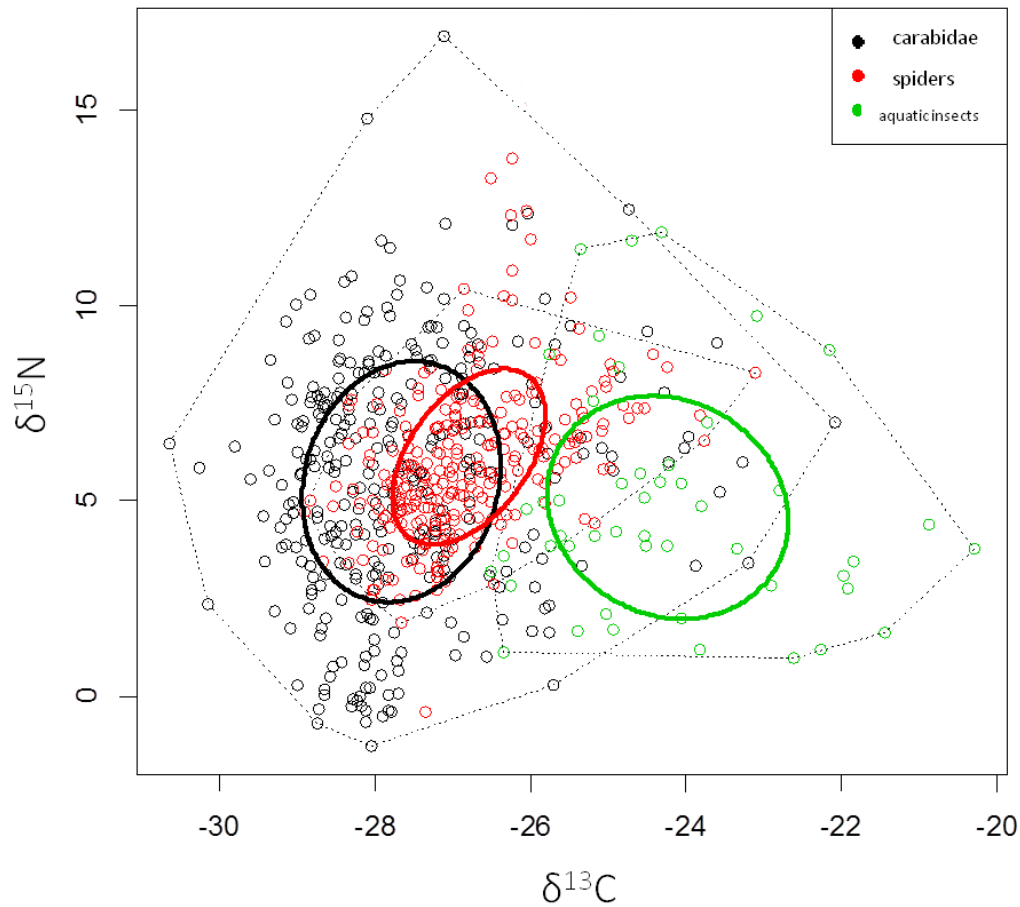
**Fig. 18** Biplot of  $\delta^{15}N$  and  $\delta^{13}C$  showing convex hull (dashed line) and  $SEA_c$  (solid ellipses) for spiders (red) and ground beetles (black; without phytophagous species)



**Fig. 19** Boxplot of  $SEAc$  for spiders and ground beetles

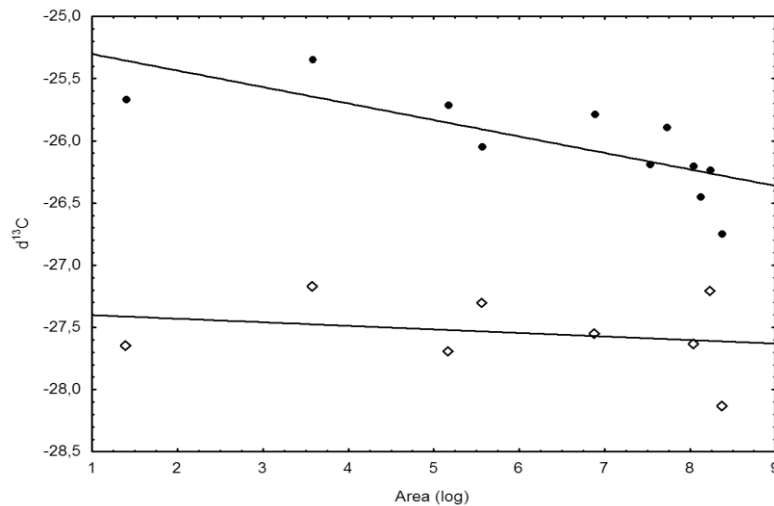
### *Spatial subsidies*

Aquatic animals were clearly distinguishable by their position in isotopic space. While there was substantial overlap in the convex hull area (TA) between aquatic animals ( $SEAc = 13.8$ ;  $TA = 46.2$ ), spiders ( $SEAc = 6.1$ ;  $TA = 51.2$ ) and ground beetles including phytophagous species ( $SEAc = 12.3$ ;  $TA = 91.6$ )(see above), the standard ellipse area ( $SEAc$ ) of aquatic animals did not overlap with that of spiders and ground beetles at all (Fig. 20)



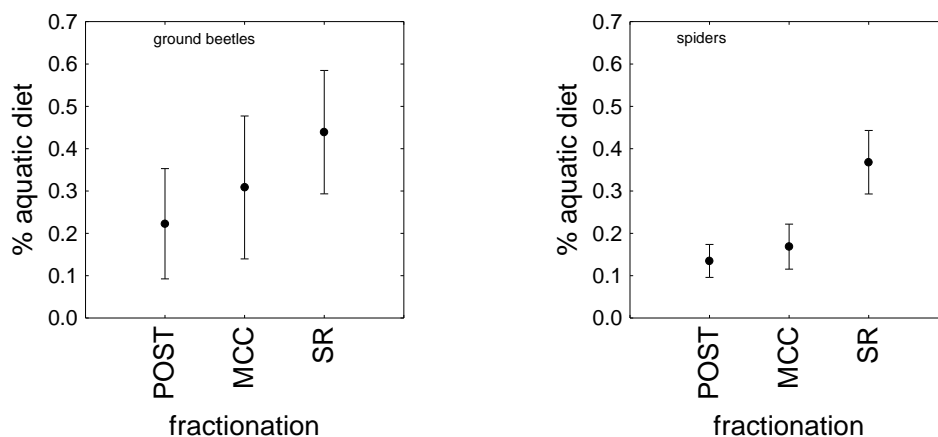
**Fig. 20** Biplot of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  showing convex hull (dashed lines) and SEA<sub>c</sub> (solid ellipses) for ground beetles (black; phytophagous species included), spiders (red) and aquatic insects (green)

$\delta^{13}\text{C}$  decreased slightly with island area in spiders ( $r = -0.34$ ;  $r^2 = 0.11$ ;  $p < 0.001$ ), but not in ground beetles ( $r = 0.10$ ;  $r^2 = 0.01$ ;  $p = 0.08$ ). Unlike in  $\delta^{15}\text{N}$  signatures, these patterns were not preserved at the species level.  $\delta^{13}\text{C}$  decreased with island area in *O. limbatum* ( $r = -0.43$ ;  $r^2 = 0.19$ ;  $p < 0.05$ ) and *N. salina* ( $r = -0.56$ ;  $r^2 = 0.32$ ;  $p < 0.05$ ), but even showed a positive relation to island area in *H. affinis* ( $r = 0.66$ ;  $r^2 = 0.43$ ;  $p < 0.001$ ). Mean  $\delta^{13}\text{C}$  signatures decreased with island size in the wolf spider *A. leopardus* ( $r = 0.76$ ;  $r = 0.57$ ;  $p < 0.01$ ), but not in the co-occurring wolf spider *P. prativaga* ( $r = -0.22$ ;  $r^2 = 0.05$ ;  $p = 0.60$ ) (Fig. 21).



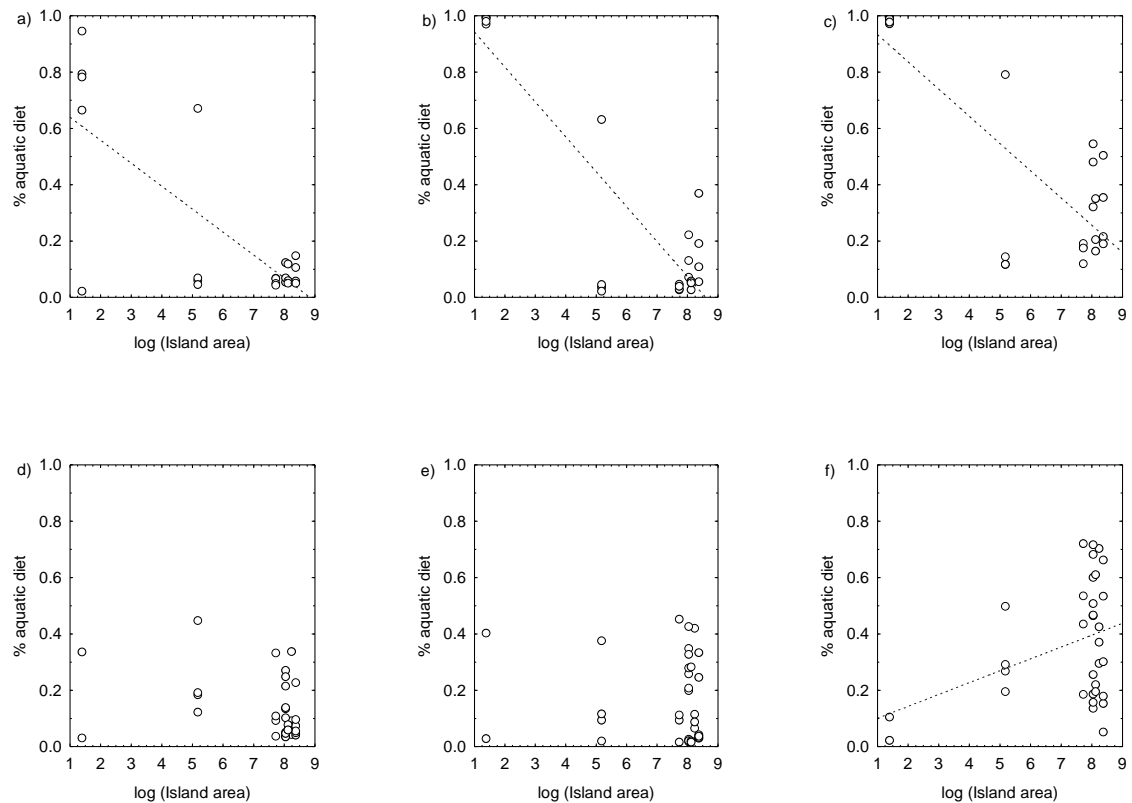
**Fig. 21** Relationship between  $\delta^{13}\text{C}$  and log-area for *A. leopardus* (solid circles;  $r = -0,76$ ;  $r^2 = 0,57$ ;  $p = 0,007$ ) and *P. prativaga* (open diamonds;  $r = -0,22$ ;  $r^2 = 0,05$ ;  $p = 0,59$ ).

The overall mean contribution of aquatic prey to the total food consumption of island arthropod communities was dependent on the assumptions of the mixing model for isotope fractionation and animal groups. For ground beetles the mean contribution averaged across islands increased from  $22.3 \pm 30.1\%$  for POST fractionation, to  $30.9 \pm 39.0\%$  for MCC fractionation, up to  $44.9 \pm 33.7\%$  for SR fractionation, but these increases were not significant (ANOVA;  $p > 0.10$ ). For Spiders, mean contributions of aquatic prey were significantly higher, when SR fractionation values ( $36.8 \pm 21.1\%$ ) were applied to the model, compared to MCC fractionation ( $16.9 \pm 14.9\%$ ) and POST fractionation ( $13.5 \pm 11.0\%$ ) values (Fig. 22; ANOVA;  $p < 0.001$ ).



**Fig. 22** Proportion of aquatic diet for ground beetles (left) and spiders (right) calculated for different scenarios of fractionation

The effect of island area on the contribution of aquatic prey differed between animal groups and model assumptions about fractionation of  $^{13}\text{C}$  and  $^{15}\text{N}$ . The percentage contribution of aquatic subsidies to the total community significantly decreased with increasing island area for ground beetles, regardless of the model assumption. For spider communities, there was a significant positive relationship between island area and the percentage contribution of aquatic prey, only when SR fractionation values were used in the model, but not when POST or MCC fractionation values were used (Fig. 23; Tab. 17).



**Fig. 23** Relationships between the proportion of aquatic diet and island area (log) for ground beetles with fractionation values from a) POST ( $r = -0.75$ ;  $r^2 = 0.56$ ;  $p < 0.001$ ); b) MCC ( $r = -0.88$ ;  $r^2 = 0.78$ ;  $p < 0.001$ ); c) SR ( $r = -0.79$ ;  $r^2 = 0.63$ ;  $p < 0.001$ ), and spiders with fractionation values from d) POST ( $r = -0.3$ ;  $r^2 = 0.09$ ;  $p = 0.09$ ), e) MCC ( $r = -0.06$ ;  $r^2 = 0.00$ ;  $p = 0.73$ ), f) SR ( $r = 0.36$ ;  $r^2 = 0.13$ ;  $p < 0.05$ )

*A. leopardus* and *P. prativaga* were the only species with sufficient island occupancy to test for a relationship between island area and percentage contribution of aquatic prey at the species level. The latter increased in *A. leopardus* with island area according to SR fractionation values, but not when POST or MCC fractionation values were applied. *P. prativaga* did not show a relationship between island area and the proportion of aquatic subsidies under any model assumption (Tab. 18).

**Tab. 18:** Results of Pearson regression for the percentage of aquatic diet and log-island area with different assumptions about fractionation of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (POST, MCC, SR) in the species *A. leopardus* (AL) and *P. prativaga* (PP).

Model assumptions	$r$ (AL)	$r^2$ (AL)	$p$ (AL)	$r$ (PP)	$r^2$ (PP)	$p$ (PP)
POST	-0.50	0.25	0.25	0.06	0.003	0.91
MCC	-0.19	0.04	0.68	0.35	0.12	0.49



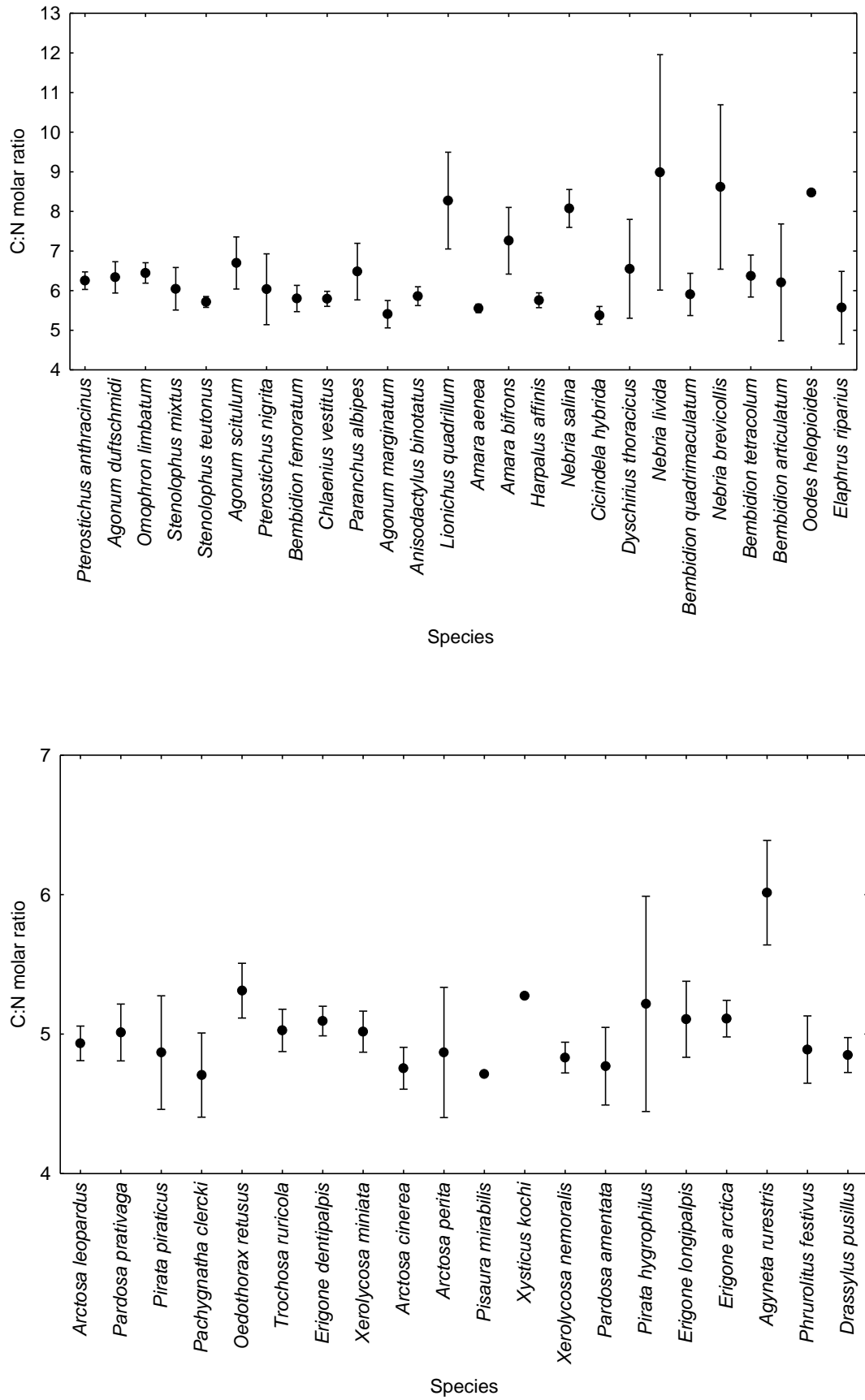
<b>SR</b>	0.94	0.88	0.002	0.37	0.13	0.48
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The most clearly distinguishable predator of aquatic animals was the ground beetle *O. limbatum*. The mixing model MixSIR revealed that at the Brüggehofsee - depending on model assumptions - 79.1 % ( $\pm 0.07$  %) of the diet of *O. limbatum* were aquatic primary consumers of the littoral, most abundantly represented by larvae within the aquatic beetle family Haliplidae. Also on small islands in the Diersfordter Waldsee, *O. limbatum* utilized aquatic subsidies represented by mayflies (Ephemeroptera), making up 82.6 % ( $\pm 0.07$  %) of their diet. On a larger island, pillbugs of the genus *Armadilidium* sp. were the most likely main food source, contributing 82.5 % ( $\pm 0.05$  %). Another predator, which fed partly on aquatic prey was *A. leopardus*. Aquatic organisms like haliplid beetle larvae contributed between 40% - 50 % to its diet on small islands in the Brüggehofsee. On these small islands, no main component of *A. leopardus* diet could be clearly identified. On larger islands of the Diersfordter Waldsee, proportions of aquatic prey of *A. leopardus* were similar (38.8 %  $\pm 0.03$  %), but the main food source were clearly terrestrial herbivores like *A. aenea* (52.1 %  $\pm 11.7$  %).

### *Stoichiometry*

Mean Molar C:N ratios significantly differed between ground beetles and spiders (Fig. 24). Molar C:N ratios were usually wider, with higher variation in ground beetles ( $6.19 \pm 1.01$ ) than in spiders ( $4.98 \pm 0.42$ ). Thus ground beetles and spiders were - with a few exceptions - distinguishable by their C:N ratios. Ground beetles had C:N ratios  $> 5.5$  while spiders had C:N ratios mostly  $< 5$ . An exception in spiders was the sheet web spider species *Agyneta rurestris* (C.L. Koch, 1836) with a mean C:N ratio of  $6.01 \pm 0.24$ . An exception in ground beetles was the tiger beetle *Cicindela hybrida* (Linné, 1758) ( $5.38 \pm 0.44$ ). The three *Nebria* spp. found in the study system, *Lionichus quadrillum* (Duftschmid, 1812) and *Oodes helopioides* (Fabricius, 17929) had exceptionally wide C:N ratios  $> 8$ .

The majority of ground beetles sampled in June had narrower C:N ratios than ground beetles of the same species, sampled in August. Increased C:N ratios in August were typically accompanied by lower  $\delta^{13}\text{C}$  signatures and  $\delta^{15}\text{N}$  signatures (Tab. 19). In the ground beetle *Nebria livida* (Linné, 1758) C:N ratios decreased by  $\sim 28$  % and  $\delta^{13}\text{C}$  signatures increased between June and August.

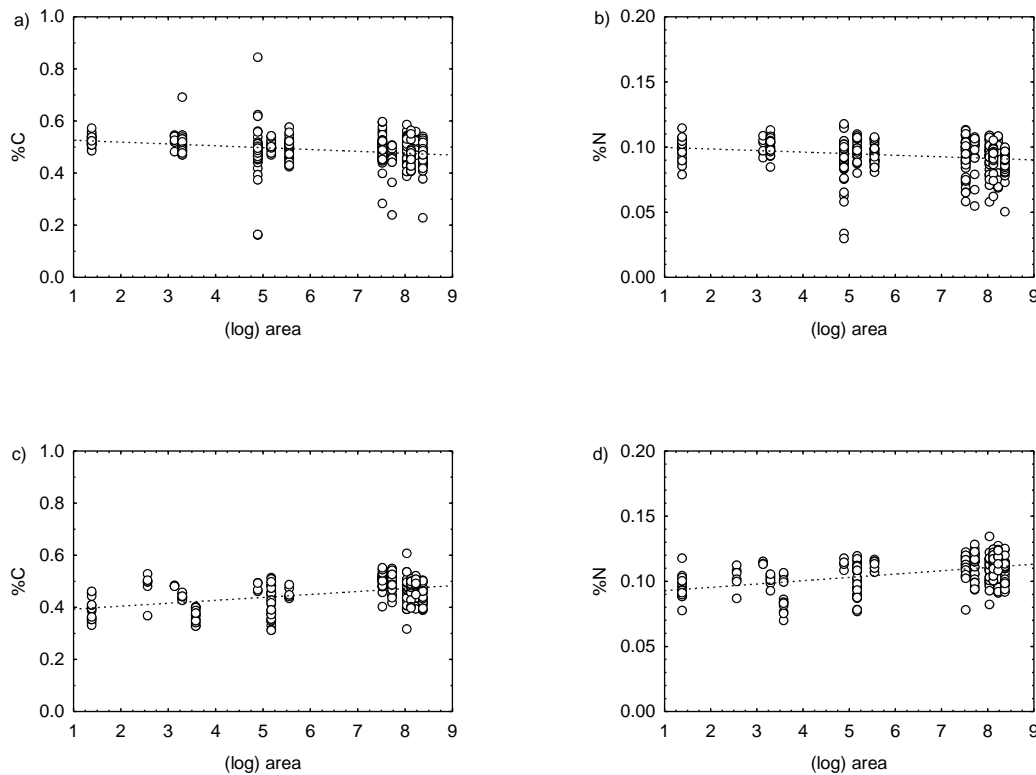


**Fig. 24** Molar C:N ratios of ground beetles (upper) and spiders (lower); note the different scaling of the y-axis.

**Tab. 19:** Comparison of molar C:N ratios,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures of several ground beetle species between June and August

Species	Island	June			August		
		molar C:N	mean $\delta^{13}\text{C}$	mean $\delta^{15}\text{N}$	molar C:N	mean $\delta^{13}\text{C}$	mean $\delta^{15}\text{N}$
<i>A. binotatus</i>	D3	5.6 ± 0.4	-28.0	9.0	8.3 ± 1.0	-28.3	8.7
	D1	--	--	--	9.8 ± 1.0	-29.2	14.1
	D2	--	--	--	9.4 ± 0.3	-28.3	10.7
<i>A. bifrons</i>	D3	7.3 ± 0.8	-27.7	11.8	7.1 ± 0.7	-28.5	6.9
	D2	--	--	--	6.2 ± 0.6	-28.1	10.9
	D4	--	--	--	5.9 ± 0.6	-28.3	3.5
	D8	--	--	--	6.2 ± 0.6	-28.9	1.9
<i>A. aenea</i>	D5	5.6 ± 0.4	-28.3	0.7	7.9 ± 0.7	-29.8	0.6
<i>C. hybrida</i>	D7	5.6 ± 0.5	-27.3	3.8	6.1 ± 0.5	-27.5	4.0
	D8	5.4 ± 0.3	-27.2	4.6	6.5 ± 0.6	-27.9	3.3
	D5	--	--	--	7.1 ± 0.8	-28.1	3.6
<i>N. livida</i>	D8	9.0 ± 1.2	-29.6	6.4	6.5 ± 0.6	-28.0	6.3

Molar C:N ratios were unrelated to  $\delta^{15}\text{N}$  in ground beetles and spiders. In both arthropod groups C:N ratios they were negatively correlated to  $\delta^{13}\text{C}$ , but the explanatory power of the model was low (ground beetles:  $r = -0.25$ ;  $r^2 = 0.06$ ;  $p < 0.001$ ; spiders:  $-0.38$ ;  $r^2 = 0.15$ ;  $p < 0.001$ ). The percentage of total carbon and nitrogen content of body dry mass decreased slightly, but significantly with island area in ground beetles (C %:  $r = 0.25$ ;  $r^2 = 0.06$ ;  $p < 0.001$ ; N %:  $r = 0.21$ ;  $r^2 = 0.04$ ;  $p < 0.001$ ). In spiders the percentage of total carbon and nitrogen content significantly and clearly increased with island area (C%:  $r = 0.44$ ;  $r^2 = 0.19$ ;  $p < 0.001$ ; N %:  $0.46$ ;  $r^2 = 0.21$ ;  $p < 0.001$ )(Fig. 25).

**Fig. 25** Relationships between relative content of carbon and nitrogen to island area (log) for ground beetles (a-b) and spiders (c-d)

## Discussion

### *Describing the Community*

The terrestrial ecosystems on the mainland and islands of the gravel pit lake system investigated in this study were found to be inhabited by an unexpectedly diverse community of 93 spider species and 84 ground beetle species. Larger islands in the Diersfordter Waldsee were inhabited by many species, which are naturally distributed in coastal dune habitats of northern Europe. The most common spider species on these islands, *X. miniata* has been described as a good indicator species for inundating mesotrophic grasslands with the presence of *Salix repens* in such coastal ecosystems (Bonte *et al.* 2002). Other spider species, common in this study can be found at the fore beaches of coastal ecosystems, like *Arctosa cinerea*, *Arctosa perita* and dwarf spiders of the genera *Oedothorax* and *Erigone* (Almqvist 1973), but also *Pardosa prativaga*, *Trochosa ruricola* and *Arctosa leopardus* (Mellbrand 2009). Many of these spider species also occur in riparian zones of European streams (Lambeets *et al.* 2005). Ground beetles from these habitats, which occurred at the Diersfordter Waldsee were *Cicindela hybrida*, *Nebria salina* and *Harpalus affinis* (Luff 1998). The most common ground beetle species, *Amara aenea* is an eurytopic species of dry grasslands. However the majority of ground beetle species were species typically found on riparian gravel banks or inundating riparian fens and temporary wetlands (Lehmann 1965; Brose 2003; Lambeets *et al.* 2008). Large proportions of the ground beetle and spider species found at the island system have long since been known as early colonizers of open casting pits, following lignite or gravel mining (Neumann 1971; Gack *et al.* 1999; Brändle *et al.* 2000; Al Hussein 2002) and arable fields (Samu & Szinetár 2002; Irmeler 2003). It is thus likely that many ground beetle and spider species were already common to the area before the restoration of the gravel pit started. Nevertheless, the restoration and landscape management implemented have achieved to preserve these communities, including many endangered species to this day. Rarefaction of the species data indicated that species lists were far from complete and that the true species richness of spiders and ground beetles was - depending on the particular island - between 40 % and 80 % higher. But the exact estimates of species richness have to be handled with caution, since jackknife estimates are sensitive to sampling coverage (Brose *et al.* 2003), which was not strictly proportional to area in this study.

According to the young age of the communities - confirmed by data on wing status of ground beetles, which will be discussed later - the high species richness might still be an overshoot of recently arrived propagules, colonizing the islands. Some of these species will probably fail to establish and species numbers will relax to lower, but rather persistent values (Simberloff & Wilson 1970). Comparing older large islands in this study with the youngest island, which had the highest species richness of ground beetles and spiders it seems that such a relaxation has already occurred. It is also important to note, that a reduction in species richness over time after initial colonization is far from being a general ecological law (Schoener 2009) and future trends of species richness and composition may strongly depend on successional development, disturbance regimes and regional meta-community dynamics (Thomas 1994). Furthermore, the highly diverse island communities are not merely explained by island biogeographic dynamics of immigration and extinction, but also by the spatial heterogeneity of environmental conditions within and between islands and lake systems. Species richness and species composition clearly differed between island centers and island shore zones, as well as between the Diersfordter Waldsee and the Brüggelhofsee.

### *Species distributions and environmental conditions*

This study clearly demonstrates how the species richness and composition of ground beetles and spider communities tracked the increasing spatial heterogeneity of environmental conditions on a group of islands with increasing area. On the islands, the spectrum of spatial heterogeneity was limited to a remarkably small set of basal environmental factors, due to the young island age and the lack of complex structural components like woody vegetation. On the smaller islands, arthropod communities were entirely composed of riparian and wetland species, since most of the soil was wet or highly humid round the year and ‘edge habitat’ like gravel shore and *Juncus* spp. dominated. As space increased, plants utilizable by herbivorous ground beetles appeared, dryer habitat areas became increasingly available and species representative of dry meadows (*A. aenea*, *H. affinis*) and coastal dunes (*Cicindela hybrida*, *Arctosa perita*, *X. miniata*, *Arctosa cineara*) were added to the community. Dry conditions were highly limited on small islands and thus phytophagous and non-riparian ground beetles had the steepest SAR - slopes (highest z values) and the lowest nestedness temperatures of all taxa and subgroups tested. Moreover, phytophagous ground beetles disproportionately contributed to the overall significance of the species area relationship of ground beetles, for the removal of only seven phytophagous species out of 63 beetle species on islands in total rendered the SAR - relationships insignificant. Accordingly, species disappeared together with their preferred habitat as island area decreased and so island communities of ground beetles and spiders were significantly nested. On the other hand, since the species richness of non-riparian, non-phytophagous ground beetles also significantly increased with area, it becomes clear, that the species area relationship of ground beetles, preferring dry conditions, was flattened by the statistical noise of riparian ground beetles, which even exhibited a slightly negative species-area trend. This may be partially because of the comparably small increase in island perimeter relative to the increase in total area. On the other hand, this phenomenon can be viewed as a small island effect (SIE) (Triantis *et al.* 2006) for riparian beetles. In this case, the number of riparian ground beetle species would be increased by some factor above the expected species richness in a species area relationship. In most cases this factor is unknown and it is still discussed how SIEs are properly detected (Dengler 2010) or if they are artifacts at best (Burns *et al.* 2009; Tjørve & Tjørve 2011), but hypotheses have been proposed that see the cause of the SIE in spatial subsidies. Allochthonous intakes of food increase the species richness on small islands beyond the level, autochthonous production would allow (Anderson & Wait 2001).

The strong positive relationship between island area and the mean drought preference of spiders reflected the environmental patterns described above. Even though shade preference values of spiders showed a stronger negative correlation to edge response values than drought preference values, the mean shade preference increased with island area at a much slower rate than mean drought preference. This again reveals gradients of moisture as the main drivers of biodiversity patterns on the gravel pit islands in this study. Combining mean preference values of species and their standard deviations can be linked to environmental heterogeneity. The standard deviation of species niche preference values can be expected to increase with island area by pure mass effects, e.g. by random passive sampling. As the number of species randomly colonizing an island increases with area, the preferences of these species will also show a higher, pure random variation. However, with random passive sampling, mean preference values for island communities should be unrelated to area in general. With non-random colonization the mean values should converge to preference values for the limiting habitat as island area increases. By using the habitat preference values calculated by Entling *et al.* (2007), I could show that these preference values obtained from large gridded data for spiders can be successfully applied to small-scaled environmental gradients. Provided the environmental gradients in moisture and shading are large enough, they can be represented by spider habitat preferences within ranges as short as 10 meters. These findings underpin the non-random and non-neutral mechanisms that lead to the

species-area relationships found for the described island system. In the study system, species were assorted to islands by matching an increasing heterogeneity of available habitats with increasing area and not via random sampling, nor through pure ‘area *per se*’ effects. It was possible to directly link species distributions and occurrences to niche properties of spiders and thereby definitely exclude neutral processes of community assembly. However, this does not mean that area *per se*, stochastic processes or mass effects did not shape the species distribution on the islands at all. Their influence might be just of minor importance in the studied system. Furthermore, it is not possible to exclude mass effects or source-sink mechanisms, in which well adapted species on the islands would be a sample from dominant species in the regional species pool (Holt 1993; Mouquet & Loreau 2003), while the niche properties of other regionally rare species could possibly better match the available habitats. It is merely possible to exclude mass effects, by which insects or spiders of nearby distinctly different ecosystems dominate the island communities through short distance dispersal. It is rather surprising, given the high abundance of e.g. the eurytopic ground beetle *A. aenea* on large islands of the Diersfordter Waldsee that not a single individual of this species was found on the nearby mainland. On the contrary, *X. miniata*, which is a wolf spider, adapted to dry environments, was found in the wet fen meadows of the mainland opposite to the islands. This obviously was the consequence of the passive dispersal of spiders as juveniles with silk threads, called ‘ballooning’. Nevertheless, from a meta-community perspective, the local community assembly on the islands was largely governed by strong species-sorting effects (Leibold *et al.* 2004). Species were literally ‘lined up’ along environmental gradients or they were assorted to patches with dissimilar environmental conditions (Whittaker 1972).

In addition, the canonical correspondence analysis was able to significantly separate groups of ground beetles and spiders between different environmental variables. The clearest separation was visible between ground beetles, dwarf spiders and wolf spider species inhabiting ‘sterile’ gravel shores and more humid vegetated shore lines or central vegetation. As an example, dwarf spiders of the genus *Oedothorax* were predominantly found on smaller vegetated islands of the Brüggehofsee, *Erigone* spp. dominated the gravel banks of islands in the Diersfordter Waldsee. But also wolf spiders and ground beetles showed strong responses to vegetation density. In CCAs vegetation density was not clearly correlated to humidity, which is not surprising for sandy islands, since wet sandy shores are often to disturbed for an establishment of persistent vegetation, while on dry sandflats of these islands, well adapted plant species could thrive due to rainfall and rooting in deeper, more moist but aerated soil layers. It is important to note, that the non-correlation of the important factor ‘vegetation density’ with humidity does not contradict the conclusions made about gradients of humidity governing the community assembly on islands of the study system. The availability of water is a very basic and fundamental requirement for any terrestrial organism and adaptations to varying conditions have driven adaptive radiation in evolution and subsequent species distribution in ecology. However, despite its importance, humidity is only one dimension in the n-dimensional hyperspace of niches, proposed by Hutchinson in 1957 (Hutchinson 1991) and local vegetation density might be a further factor to select between species adapted to similar conditions of humidity. In the present study the influence of vegetation density might have been expressed in analyses of species niche preferences as the influence of shading or habitat openness, respectively. Indeed, in the dataset of Entling *et al.* (2007), *Erigone arctica* (White, 1852) and *Erigone longipalpis* (Sundevall, 1830) were the two species with the lowest tolerance to shading. In the CCA results of the present study they aligned with the factor ‘gravel shore’, which was negatively correlated to ‘vegetation density’.

These findings are in line with the results of the analysis of co-occurrence in the study area. The two measures applied, C-score and Checkerboard Score, were found to be usually higher than expected from random (Gotelli & McCabe 2002), indicating less co-occurrence than expected by chance. These

patterns are thought to be caused by interspecific competition, so that species are less likely to co-occur, because they are unlikely to co-exist (Diamond 1975a). Effectively, both measures are unable to inform about the underlying mechanism of co-occurrence. Indeed, higher values of C-Score and Checkerboard pairs, i.e. species segregation can also be caused by environmental heterogeneity (Bell 2005). Species thus can co-occur less than expected by chance, because they are adapted to different environmental conditions and thus never occur in the same habitat. Also neutral models were also able to reproduce these patterns (Ulrich 2004). C-Score and Checkerboard score were both higher than expected by chance in the island system of the Diersfordter Waldsee. Although these findings did not directly confirm the mechanism of species sorting or niche separation, the results of the null model analysis were in general agreement with co-occurrence patterns generated by environmental heterogeneity.

Despite these results and the importance of increasingly available dry habitats on large islands for the species area relationships and patterns of nestedness in ground beetle and spider communities, moist habitats contributed disproportionately to the overall species richness of the lake-island system. Although total activity densities of spiders and ground beetles were uniformly distributed across island zones, species richness on larger islands was higher at the shore zone in both arthropod groups. In total, still 36 of the 50 spider and ground beetle species I calculated edge response values for, had a positive edge response value, i.e. these species showed higher activity densities at the shores than in the islands centers. In spider communities, species edge response values were highly correlated to their standardized values of drought and shade preference, i.e. “edge loving spiders” indeed preferred the moist and exposed conditions found on the shore and were not solely “random edge walkers” (Ries & Sisk 2010).

Explanations for higher species richness in shore habitats might be ready at hand. It can partly be explained by overlapping communities of dry and moist habitats. With increasing area, a few species adapted to xeric conditions were added, which quickly increased to dominate the total island communities in terms of abundance. The phytophagous ground beetle *A. aenea* and the wolf spider *X. miniata* were found in island centers and shore zones with similar high densities, peaking in the middle zone. This most likely represents a ‘doughnut effect’, i.e. individuals from the center walk towards the edge and back, thereby accumulating as they meet in-between the two habitats. Also highly mobile xerophilic species, as the tiger beetle *C. hybrida* were frequently found at the shore zone. In contrast, riparian species were in general strongly restricted to the shore zone, even if highly abundant, indicating spatially strongly restricted movement ranges of riparian species. The uniform distribution of the activity density of ground beetles and spiders across zones was therefore in part a spillover effect of the most abundant and mobile xerophilic species. However, in the warm summer months, sparsely vegetated gravel shores can change from wet, wave-pounded habitats to hot and xeric environments within hours and regarding the climatic niche breadth, become part of the natural foraging range of these xerophilic species.

Additionally, shores are more frequently disturbed by wave action and thus are more frequently recolonized, not allowing for long- term exclusion through competition (Shea *et al.* 2004). Also species that fall into water and survive, are washed ashore contributing to the number of rare species in the shore assemblage, which has been termed the ‘beachcomber effect’ by some authors (Buckley & Kneidlans 1986). Species adapted to the abiotic conditions at gravel shores might vary in their responses to pulsed spatial subsidies from aquatic systems (Paetzold *et al.* 2006), which could further enhance biodiversity (Chesson *et al.* 2004; Holt 2008). Indeed, the results of stable isotope analysis - discussed later - indicated that the utilization of spatial subsidies was restricted to a small subset of riparian spider and ground beetle species. However, the true underlying patterns were likely much more complex and more difficult to identify. One reason was the occurrence of satellite species or

singletons, respectively. Rare species contribute much to the overall species richness in nearly all ecosystems, known as the ‘tails of rank abundance distributions’, (Murray *et al.* 1999). Of the 39 ‘satellite ground beetle species’ ( $I \leq 3$ ) found on larger islands, 22 (56.4 %) were found at the shore, but only 12 (30.8 %) of them could be classified as riparian species. For ground beetle communities this might indicate an assembly mechanism based on a higher species turnover on shores. However, in spider communities, 15 (39.5 %) out of 38 satellite species occurred in the center and proportions decreased toward the shore (B: 31.5 %; A: 29 %).

In other words, more than half of the ground beetle species found on the shore were rare at the studied sites, while the majority of spiders in shore habitats belonged to common species, pointing at either two different mechanisms or two different stages of community assembly for spiders and ground beetles. These mechanisms might reflect the different dispersal capabilities of winged ground beetles and passively dispersing vagrant spiders. While, due to their flying capabilities, ground beetle communities are potentially able to recruit species from a wider geographic range (Ås 1984; Kotze & Niemelä 2002a), recruitment of vagrant spider species might occur only in a more narrow regional context (Schmidt *et al.* 2008). Spiders might therefore have dispersed between the frequently recolonized shores within the lake system, while ground beetles also could have reached the two lakes from a diversity of ecosystems at the Lower Rhine area. Indeed, in this study, species occupancies for spiders showed a correlation to edge responses, i.e. spiders preferring moist habitats were more widespread in the study system than xerophilic species (Fig. 13 h), while for ground beetles no such relationship existed. Furthermore, ranked species occupancy distributions showed that the three most common shore dwelling spiders, *A. leopardus*, *T. ruricola* and *P. prativaga* occupied higher proportions of islands than even the most widespread ground beetle species, *A. binotatus* and *S. teutonius*. It has been long since known, that ground beetles are unable to overwinter in riparian shore habitats that are flooded in winter and therefore recolonize the shore habitats every year anew (Lehmann 1965; Thiele 1977; Holeski 1984). However, in the studied system, shore habitats were not inundated regularly and teneral of several riparian *Bembidion* spp. were found on island shores, clearly confirming stable resident populations in these habitats.

#### *Potential impacts of dispersal limitation on species distribution*

Despite the great number of studies on oceanic islands (Lomolino & Weiser 2001), it has been criticized that in particular these oceanic islands are unsuitable for testing ecological theories, since most of them are anthropogenically altered in some way (Walter 2004; Kier *et al.* 2009). Another problem of studying island biogeography on isolated oceanic islands is speciation or the high prevalence of endemism, respectively. Some authors demonstrate that increasing species richness on oceanic islands does not lead inevitably to higher extinction rates but can also lead to higher rates of specification (Emerson & Kolm 2005), while others argue that correlations between species richness and endemism co-correlate with population persistence and abiotic factors (Cadena *et al.* 2005; Pereira *et al.* 2007). Additionally, speciation rates might counteract low immigration rates on large isolated islands, potentially distorting the patterns proposed by IBT (Weigelt & Kreft 2013). However, there have been a great number of studies that investigated patterns of species richness on islands that lack speciation due to their close vicinity to the mainland. On some oceanic archipelagos and lake islands, immigration rates from the nearest mainland are so high that evolutionary diversification is virtually overridden (but see Camin & Ehrlich 1958). On these types of islands, arthropods, most notably insects and spiders have been investigated to test a diversity of ecological theories (e.g. Strong & Rey 1982; Toft & Schoener 1983; Niemelä *et al.* 1987). In a row of studies, the impact of dispersal capacity on species richness patterns and colonization capabilities was investigated in communities of ground beetles in the archipelago of the Åland Islands of Sweden and Finland. Ground beetles show



intra- and inter-specific variation in their dispersal capacities due to differences in hind wing development (den Boer 1990). Macropterous and brachypterous species exist as well as dimorphic species and such that exhibit flight muscle atrophy after the colonization of a new habitat (Darlington 1943; Kavanaugh 1985; Aukema 1995). It has been long since known, that macropterous ground beetles are the first to colonize new habitats (den Boer 1970; Meijer 1974). However, contradictory findings exist regarding their better colonization success on islands (Ranta & As 1982; Niemelä *et al.* 1988). This is in part considered to be related to a tradeoff between dispersal capability and success of population establishment (Cadotte *et al.* 2006). Species that invest more energy into dispersal through hind wing development potentially have lower amounts of energy available for competition in the struggle to successfully establish new populations in recently colonized habitats. Accordingly, macropterous species have wider distribution ranges, while brachypterous species have higher regional occupancies (Gutiérrez & Menéndez 1997; Zalewski & Ulrich 2006) and some studies find higher proportions of brachypterous beetles on islands than on the adjacent mainland (Kotze *et al.* 2000). Also turnover rates as year-to-year variation of ground beetles community composition on islands have been shown (Kotze & Niemelä 2002b). On lake islands of Masuria in Poland, higher turnover rates on small islands were demonstrated as younger population age, due to the higher proportion of macropterous individuals in the populations of the ground beetle *Pterostichus melanarius* on small islands (Zalewski 2004).

The prevalence of macropterous ground beetle species on these young island systems in contrast to the higher proportions of brachypterous ground beetle species on the mainland meets general expectations of island biogeography, with strong dispersers colonizing islands first (MacArthur & Wilson 1967; Brown & Kodric-Brown 1977) and matches empirical observations of macropterous ratios in young ground beetle populations (den Boer 1970; Desender 1989; Niemelä & Spence 1999) and mainland - island differences between ground beetles communities (Kotze *et al.* 2000).

Apparently, the studied islands were too young to observe a systematic variation of macropterous beetle ratios with area, as was found in Polish lake island systems (Zalewski 2004). Despite the close vicinity of the adjacent mainland, only few brachypterous individuals had colonized the islands and showed a rather idiosyncratic occurrence. On many small islands, wing dimorphic species made up > 15 % of the community but the proportion of macropterous individuals in these populations was 100 %. This study thereby supports the general theory through findings from newly created habitats - a rare perspective at ecological time-scales. Thus, it was observed that, although dispersal power is obviously the most important factor for an initial colonization of islands, habitats were filled according to species specific habitat preferences even at early stages of species immigration. This has important implications for community assembly, but also for ecosystem function and its resilience after disturbance. If empty niches within a habitat patch are quickly filled by highly adapted species with strong dispersal capabilities, niche partitioning might predominate mechanisms of coexistence. Competition would have been low in early stages of the islands colonization, decreasing probabilities of extinctions, allowing for very early equilibria in species richness and slow turnover rates with dramatic changes in species composition. This has likely been an important selection pressure on the evolution of wing-dimorphism in ground beetles (Aukema 1995), which enables strong priority effects after colonizing an empty habitat patch by reallocating consumed energy from dispersal to reproduction within the population via flight muscle atrophy (Zera & Denno 1997; Fukami 2004). Nevertheless, still nutrients and energy are invested into wing development per se, which might contribute to macropterous species being inferior competitors during the succession of habitat colonization. The low incidence of brachypterous ground beetle species on the islands is also remarkable, concerning the low isolation of the islands from the mainland, where up to 63 % of the species were brachypterous. While the passive dispersal of wingless ground beetles in the drift of the

Baltic Sea (amenohydrochoric) has been described and examined by several authors to exceed 10 km (Palmen 1944; Ås 1984; Niemelä *et al.* 1988), it seems that crossing a few meters of standing lake freshwater has been a rare event, even in 10 years. It might be that the 'standing' of the lake water has interfered with a passive dispersal of organisms but also fish predation in the littoral macrophyte beds might have been a strong obviation of dispersal on the lakes neuston. Many brachypterous ground beetle species that were missing on islands inhabited the leaf litter layer of alluvial forest patches on mainland sites. A leaf litter layer is missing on most islands, due to wind exposure and lacking structure. On large islands of the Diersfordter Waldsee even the accumulation of detritus of annual plants has been precluded by strong winds in winter and spring.

The slope of the species area relationship of spiders and ground beetles were not strikingly different. But the slope of vagrant spiders was steeper than that of ground beetles, while Linyphiidae had no SAR. Instead, their density increased with decreasing island area. This pattern points at the variation of species area slopes as a result of different dispersal capacity of organisms. In particular the frequently disturbed and washed small islands of the Diersfordter Waldsee were inhabited by dense populations of *Erigone* spp., which are able to balloon as adults and quickly colonize new and recently disturbed habitats (Bonte *et al.* 2004). Excluding these Linyphiidae with high dispersal power from SARs, a low diversity and often also low densities of vagrant spiders like Lycosidae remained on smaller islands, thereby steepening the slope of the SAR ( $z = 0.21$ ). Thus, small dwarf spiders of the genus *Erigone* contributed substantially to the initial species richness of spiders on small islands, flattening spiders SAR ( $z = 0.15$ ) to the shape of SARs of active flyers like mactopterous ground beetles ( $z = 0.11$ ), which were surprisingly diverse on small islands. The low numbers of dwarf spider species and individuals on larger islands might also reflect the steep SARs of wolf spiders, which prey extensively on small Linyphiidae (Snyder & Wise 1999). At last, disturbed soils and habitat openness might have been the major factor contributing to the distribution of *Erigone* spp. on the islands, since their density was highest on the newly created island, which was medium-sized and inhabited several populations of wolf spider species.

## From Communities to food webs

### *Stable isotope analysis*

The results show a clear increase of food-chain length with island area in a diverse arthropod community on man-made lake islands. Due to the relatively small size of the lake islands and extensive sampling, it was possible to test the hypothesis of a relationship between food-chain length and area in a system that was previously unexplored. Up to date, effects of area on food-chain length in terrestrial systems have been tested in a single study, which analyses food-chains on islands of the Bahamas (Takimoto *et al.* 2008). The missing of top predators on small islands of the Bahamas as well as the underlying dynamics between anolis lizards and orb spiders in the system have been known for more than 25 years (Schoener & Toft 1983; Spiller & Schoener 1988). In contrast, the present study therefore confirms the practicability of the method to estimate food-chain length in diverse, previously unexplored arthropod communities. However, despite the clear resulting patterns in mean and maximum trophic position, the complexity and spatial turnover of the arthropod communities between islands made it difficult to reveal the proximate underlying mechanisms. Larger spiders of the species *Trochosa ruricola* were widespread in the system and also found on small islands in low numbers. Although this species was unlikely to establish stable populations on the smallest islands, it was consistently found at the top of the island food-chains, so that insertions of intermediate predators and/or intra-guild predation on larger islands are the most likely structural mechanisms of food-chain

elongation. Since species compositions and population sizes varied between islands, these insertions of intermediate predators and/or intra-guild prey were almost certainly no single prominent feature of particular species and their trophic positions, repeated across islands. They were rather casual constellations of intra guild predation and omnivory, depending on the local species composition of spider and ground beetle communities. Candidates for intra-guild prey or intermediate predators on larger islands were the ant species *Lasius niger* and juveniles of the highly abundant lycosid spider *Xerolycosa miniata*. The latter spider most likely preyed on herbivorous ground beetles like *A. aenea* and *H. affinis*. *L. niger* and *X. miniata* were typically found one trophic level above, but never higher than the typical herbivore prey with the same variation in  $\delta^{15}\text{N}$ . Although  $\delta^{15}\text{N}$  was positively related to edge response values and the clear relationship between island area and the contribution of aquatic prey to food webs, there was no consistent pattern between animal groups and islands, which would justify the assumption that  $\delta^{15}\text{N}$  signatures of spiders and ground beetles on small islands were systematically altered by spatial subsidies from the aquatic environment. Thus no respective correction was implemented into the calculation of food-chain length, as was done by Takimoto *et al.* (2008). Correlations between  $\delta^{15}\text{N}$  and edge response suggest that such an influence would have slightly elevated  $\delta^{15}\text{N}$  values of predators on small islands, thereby potentially flattening the slope of the FCL-Area curve. In the case of this study, FCL would have increased at a slightly faster rate than demonstrated with the algorithm applied. Furthermore, introducing spatial subsidies to the concept of food-chain length makes clear, how predators integrate multiple channels of energy and nutrients and how fuzzy the concept of ‘trophic levels’ is. Which trophic level can be assigned to a spider that feeds as a predator on a plant - herbivore food-chain, as a top-predator on the ‘4<sup>th</sup> level’ of a detrital food chain and as a top predator of several aquatic insects from various trophic levels at the same time? The answer might be something like 3.6 to some, but then again one could ask for the variation of trophic levels on the population level. One must be careful, when interpreting data on trophic levels, gathered by stable isotope analysis, when the multiple food-chains integrated by predators might also vary in their enrichment per trophic level between and within different food-chains. The number of true trophic levels - distinct or continuous - heavily depends on the assumptions about fractionation of  $\delta^{15}\text{N}$  applied, but the FCL-area relationship is not affected until the enrichment of  $\delta^{15}\text{N}$  varies systematically with island area. There is no reason to assume such a systematic variation, but it is important to remember that the true enrichment factors are unknown and might be subject to substantial variation, caused by a wide range of factors (Boecklen *et al.* 2011).

Further uncertainties about the magnitude of a FCL-area relationship are the findings of a negative correlation of  $\delta^{15}\text{N}$  and island area which was confirmed across all trophic levels, i.e. for plants, detritus, ground beetles (excluding herbivores) and spiders. Hyodo and Wardle (2009) found a similar pattern for plants and leaf litter, but not for arthropod consumers, on boreal lake islands in Sweden. They explained their results as a consequence of differences in ‘ecosystem retrogression’ (Peltzer *et al.*) between small and large islands. These differentiation processes due to different fire histories took hundreds or thousands of years (Wardle *et al.* 1997). In contrast, the man-made islands in our study were created approximately 10 years before the first survey and never even reached the successional stages of forest vegetation. There are several alternative explanations for these patterns, which do not exclude one another. The negative correlation of  $\delta^{15}\text{N}$  and island area can be explained with a higher dependency of plants on rainwater on larger islands. The small islands in the size range of our study system were saturated with lake water during the whole year, providing plants mostly with nitrogen from lake water with positive  $\delta^{15}\text{N}$  signatures. In contrast, the dry sandy flats on large islands had a low water holding capacity, and atmospheric nitrogen, deposited by rain water was likely the only nitrogen source that was temporary available for plants.  $\delta^{15}\text{N}$  plant signatures typically decrease to negative values in areas with high precipitation (Handley *et al.* 1999; Hartman & Danin 2010) and Freyer (1978, 1991) has shown that  $\delta^{15}\text{N}$  of nitrate species in rainwater show a systematic seasonal

variation with the lowest values in summer. If this variation in  $\delta^{15}\text{N}$  of nitrogen availability for plants on larger islands translated into a high variation in the  $\delta^{15}\text{N}$  of the plant-baseline, our results might be an imprecise temporal snap-shot. However, since we used herbivores as the base of the food-chain on larger islands, this hypothetical temporal variation in  $\delta^{15}\text{N}$  of the plant base line was likely buffered by temporal averaging of the  $\delta^{15}\text{N}$  plant signals by the herbivores (O'Reilly *et al.* 2002). Higher  $\delta^{15}\text{N}$  signatures of plants and animals on smaller islands could have also been caused by higher levels of denitrification, a process in which during the conversion of nitrate( $\text{NO}_3^-$ ) higher proportions of light  $^{14}\text{N}$  are incorporated into molecular gaseous nitrogen( $\text{N}_2$ ), while higher proportions of heavy  $^{15}\text{N}$  will remain in the wet and anoxic soils (Wada *et al.* 1975). Additionally, aquatic animals contributing to the island food-webs and nutrient dynamics in relatively higher proportions could have increased  $\delta^{15}\text{N}$  signatures in animals and plants on small islands.

Small islands with an obviously high coverage of bird feces were excluded from the regression of  $\delta^{15}\text{N}$  and island size. The transport of nutrients by birds can alter the flux of nutrients between freshwater and terrestrial systems (Bildstein *et al.* 1992; Ueno *et al.* 2006). The enrichment of whole food webs by the deposition of bird feces has been found in insular and coastal marine systems (Barrett *et al.* 2005; Caut *et al.* 2012). Bird feces have even been found to increase the  $\delta^{15}\text{N}$  signatures of aquatic primary producers near bird colonies (Wainright *et al.* 1998). These inputs have great impacts on local ecosystems through bottom-up facilitation via plant growth (Caut *et al.* 2012). Nutrient subsidies to islands and coastal systems are so widespread and common that the alteration of bird nesting choice via the introduction of invasive plants is considered to deplete nutrients in coastal ecosystems throughout the tropics (Young *et al.* 2010). However, recent studies have shown that nesting and foraging birds can also have negative impacts on plant species richness (Kolb *et al.* 2012). Furthermore, if foraging birds migrating between inland and coastal systems are subsidized by human agricultural activities, their impact on coastal systems (Jefferies *et al.* 2004), but also inland ecosystems can be increased (Van Eerden *et al.* 2005). The deposition of bird feces has clearly altered the isotopic signals of some small islands in the present study, although due to the high variation in  $\delta^{15}\text{N}$  signatures of small islands, the extent of this enrichment was difficult to quantify. Isotopic signatures of bird feces ranged from 6 ‰ to 15 ‰ for  $\delta^{15}\text{N}$  and from 13 ‰ to 28.5 ‰ for  $\delta^{13}\text{C}$ . Bird feces, enriched in  $\delta^{13}\text{C}$  to values of 13 ‰ were likely deposited by anserine birds, which fed on agricultural maize and bred on gravel-pit lake islands. In particular on small islands of the Diersfordter Waldsee, bird feces led to an unusually high enrichment of collembolans, so that they appeared at the top of the isotopic space. Dwarf spiders of the species *E. dentipalpis*, known to feed on collembolans, surprisingly had lower  $\delta^{15}\text{N}$  signatures than their potential prey. This could indicate that the small islands were recently disturbed and re-colonization was in progress during the sampling period, so that dwarf spiders had arrived after the collembolans and the majority of individuals had not yet incorporated enough collembolans of the bird island as prey into their diets (See Appendix). Enriched  $\delta^{15}\text{N}$  signatures were also found in ground beetles of the species *E. riparius*, caught on small islands of the Brüggehofsee in August, which were still inundated in June. These small islands were rapidly covered with bird feces and the enriched signal seemingly propagated immediately through the food web.

Stable isotope analyses showed a clear enrichment in  $\delta^{13}\text{C}$  signatures of benthic aquatic organisms - autotrophic or heterotrophic - that was clearly distinguishable from most terrestrial organisms. In addition, aquatic insects had a higher variation in  $\delta^{13}\text{C}$  signatures and a lower variation in  $\delta^{15}\text{N}$  signatures than terrestrial organisms. On the contrary, pelagic zooplankton and POM of the Diersfordter Waldsee were clearly depleted relative to most terrestrial plants and animals. These patterns of  $\delta^{13}\text{C}$  signatures are in agreement with the different fractionation of  $^{12}\text{C}/^{13}\text{C}$  in benthic and pelagic habitats described in the literature (France 1995; Hecky & Hesslein 1995; Doi *et al.* 2010).

However, detrital and herbivore pathways were indistinguishable in our study, since plants and detritus had very similar  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures. The variation of  $\delta^{15}\text{N}$  within groups of animals and sometimes even within species was extremely high, spanning several trophic levels in some cases. For ground beetles, this seemed to be a general pattern. Similar high variations of  $\delta^{15}\text{N}$  were found on lake islands in Poland (Zalewski *et al.* 2014). The higher variation of  $\delta^{13}\text{C}$  in ground beetles compared to spiders is obviously due to the existence of phytophagous, omnivorous and predatory species within this group. Thus, ground beetles spanned a wider range of trophic levels than spiders. Results of the mixing models for ground beetles revealed a high degree of omnivory even on the level of alleged herbivores. On island D7 and D8, *A. aenea* and *H. affinis* were shown to partially feed on collembolans. From the analysis, it could not be definitely said, if the feeding on collembolans took place at adult stages during these beetles life histories. For *A. aenea*, which is otherwise considered to be purely phytophagous, it is known that larval stages are omnivorous (Hurka & Jarosik 2003). It seems convenient that unproductive environments are first colonized by omnivorous species, which are capable of supplementing their predominantly herbaceous diet with smaller prey organisms or by scavenging.

Measures of niche width, standard ellipses and convex hull area were still higher for ground beetles, when phytophagous ground beetles species were removed. 65 % of the niche width of spiders overlapped with that of ground beetles, suggesting exploitative competition between high proportions of the two communities, but also a high potential for intra-guild predation. Some species like the ground beetle *S. teutonius* spanned a  $\delta^{15}\text{N}$  range of at least three trophic levels. Extremely high variation of  $\delta^{15}\text{N}$  was also found in *A. binotatus* and *C. vestitus*. There are two possible explanations for this high variation in  $\delta^{15}\text{N}$  signals. The first is omnivory on the population level. The ability of a species to feed on more than one trophic level - 'omnivory' *sensu* Pimm and Lawton (1978) - would thus be expressed as a variation in diet between individuals of a population in response to intra-specific competition (Svanbäck & Bolnick 2007), rather than the feeding on different trophic levels by the same individuals. Additionally, intra-specific variation in food preferences might be accompanied by variation in  $\delta^{15}\text{N}$  enrichment with prey type (see Boecklen *et al.* 2011). The second explanation assumes a constant turnover of individuals within ground-beetle populations of an island. Thus, the variation in  $\delta^{15}\text{N}$  signatures would reflect the spatial variation of  $\delta^{15}\text{N}$  in the surrounding environment and after feeding in one place with distinct isotopic signatures, ground beetle individuals would then disperse to find new resources in other places, which are maybe already inhabited by conspecifics. Ultimately, it could be a mixture of both mechanisms. In our data, plant species also showed high interspecific variation of  $\delta^{15}\text{N}$  within islands and considerably high intraspecific variation between islands. Consequently, generalist herbivory could also have contributed to a high variation in  $\delta^{15}\text{N}$ . It is difficult to specify assumptions, which would help to separate these mechanisms and future studies have to further elucidate the high variation of  $\delta^{15}\text{N}$  signatures in populations of ground beetles. In this study the intraspecific variation of  $\delta^{15}\text{N}$  in spiders was much lower, so that an individual variation in diet within populations of omnivorous beetles could be a likely explanation. If intraspecific variation of  $\delta^{15}\text{N}$  reflected a high turnover of individuals within a population, variation in  $\delta^{15}\text{N}$  should be higher on small islands, which have generally a higher turnover, but no such relation was found for the island system in this study.

$\delta^{13}\text{C}$  signatures were significantly correlated to  $\delta^{15}\text{N}$  values in total, indicating a general enrichment of  $\delta^{13}\text{C}$  with increasing trophic level in the majority of trophic interactions.

The interpretation of stable isotope results to elucidate the detailed food web structure and identify 'who is eating whom' was quite difficult in this study, because the proportional contribution of a prey organism to the diet of a potential predator strongly depended on the assumption of fractionation applied to the mixing model. Furthermore, the standard deviations of the proportions calculated by the

mixing models were very high, regardless of assumptions about fractionation. For example on the smallest island, it completely depended on fractionation assumptions, if the ground beetle *A. duftschmidi* fed entirely on aquatic larvae of haliplid beetles (MCC and SR model) or entirely on the small beetle *C. seminulum* (POST model), that scavenges on algae and aquatic detritus on island shores. Distinguishing direct and indirect pathways of aquatic subsidies and identifying the true trophic level of *A. duftschmidi* were therefore impossible. Also the relative contribution of aquatic subsidies to terrestrial food webs as such was impossible to be accurately quantified without knowledge about the true enrichment factors of  $^{13}\text{C}$  and  $^{15}\text{N}$ . Depending on model assumption the proportion of aquatic subsidies consumed ranged from 22 % to 44 % in ground beetles and from 13.5 % to 37 % in spiders. The proportion of aquatic prey in diets of spiders and ground beetles was always highest, when the SR fractionation values were applied. Furthermore, effects of area on the contribution of aquatic subsidies were dependent on model assumptions and animal group. While ground beetles, regardless of the model, showed a strong area effect on the relative contribution of aquatic prey, spiders were significantly affected by area only when SR fractionation values were applied to the model. Moreover, for ground beetles all models yielded negative relationships between island size and the relative contribution of aquatic diet, while in spiders the SR model yielded a positive relationship between island area and relative use of aquatic subsidies. The significant differences in the application of the SR fractionation values compared to the MCC and POST fractionation values were rooted in the depletion of  $^{13}\text{C}$  per trophic level. Since due to its benthic origin, the aquatic prey in this study was enriched in  $^{13}\text{C}$  relative to the terrestrial predators, a depletion of  $^{13}\text{C}$  per trophic level as in the SR model increased the proportion potentially utilized by terrestrial ground beetles and spiders.

Nevertheless, the high proportions of aquatic subsidies to small islands food webs supplement the concept of subsidized island biogeography, proposed by Anderson and Wait (2001) by the fact that aquatic subsidies on small islands could potentially increase food-chain length by stabilizing otherwise prey-limited predator populations. However, the greater variation of food chain length on small islands indicate that unstable predator prey mechanisms could be the rule on small islands (Holt *et al.* 2009). Additionally, the present study showed a small island effect for riparian ground beetles, which could be explained with the greater relevance of spatial subsidies, but it is impossible to prove spatial subsidies as the definite cause, since data for other explanations (e.g. higher turnover) are not available.

In the studied system, the numbers of ground beetles and spider species, utilizing aquatic prey was low, compared to similar studies in riverine (Paetzold *et al.* 2006) or marine systems (Paetzold *et al.* 2008; Mellbrand *et al.* 2011), although studies in lakes for direct comparison are scarce (Gratton & VanderZanden 2009). Only a few species could be shown to make strong use of aquatic prey, which were *O. limbatum* and *A. leopardus* and *A. cinerea*. Other species, like *Bembidion* spp. and *Pardosa* spp., which have been identified to feed extensively on aquatic prey in other studies (Paetzold *et al.* 2005; Mellbrand 2009), have not been found to do so in this study. Also indirect trophic pathways, which are known from stream systems, could not be identified within the island food-webs. Members of the family Tetrigidae (Mudhoppers), which were found to feed on algae washed ashore in coastal systems (Bastow *et al.* 2002; Gröning *et al.* 2007), predominantly fed on terrestrial mosses in our study. Nevertheless, the *Tetrix* spp. contributed to the prey of *A. perita*, both being species characteristic of coastal dune systems (Bell *et al.* 1997; Gröning *et al.* 2005). Additionally, the utilization of aquatic prey might strongly depend on the exact timing of pulsed spatial subsidies. The hatching of aquatic insects is mostly restricted to short but intense periods early in the year and diet shifts might have already occurred in most species at the time of our sampling due to the low availability of aquatic prey.

Intriguingly, the effects of area on  $\delta^{13}\text{C}$  signatures contradict the effects of area on the proportion of aquatic prey, resulting from the mixing model. While  $\delta^{13}\text{C}$  signatures of spiders were in line with the increasing use of aquatic prey with decreasing islands area, the results of the mixing models were not. In fact, the mixing models with SR fractionation indicate, that the consumption of aquatic prey increased with increasing island area, especially in *A. leopardus*.

Nevertheless, for ground beetles, this study could clearly confirm the hypotheses that island communities depend more strongly on spatial subsidies from the adjacent aquatic environment with decreasing area. For spiders such a relationship is only supported by a negative relationship between island area and  $\delta^{13}\text{C}$  signatures. The response to spatial subsidies has been found to vary between ecosystems, with lakeshores being less affected than streams and coastline habitats (Marczak *et al.* 2007). Furthermore, in this meta-analysis the response of the recipient community was strongly affected by the mass ratio of aquatic subsidy to autochthonous production. In the present study, small islands likely had a smaller basis of food supply for higher trophic levels, because dominant and abundant autochthonous herbivores like *A. aenea* and highly abundant social insects like ants were missing. On the contrary, these highly abundant insects were uniformly distributed between island zones on larger islands and spilled over to the shore habitats, where they contributed to the consumption of riparian ground beetles and spiders. The relations of  $\delta^{13}\text{C}$  signatures to area in the riparian spiders *A. leopardus* and *P. prativaga* are in good agreement with these findings. Assuming, that increasing  $\delta^{13}\text{C}$  signatures of *A. leopardus* with decreasing island area point at a higher consumption of aquatic prey on small islands, such a relationship cannot be found for *P. prativaga*, although both spiders share the same habitat on small islands and according to their edge response values frequently occur together in shore habitats of larger islands. This different response to aquatic subsidies can be explained by different foraging behavior of the two spider species. The sensitivity of *A. leopardus* to ratios of allochthonous to autochthonous production might reflect its low prey specificity due to a sit and wait strategy. In contrast *P. prativaga* has been shown to be a highly selective predator, which is capable of “quasi-homeostatic” regulation of protein/fat ratios by prey choice alone (Jensen *et al.* 2011). It seems appropriate to think of shore habitats like gravel banks or fore beaches as unproductive, sterile environments, which are subsidized from adjacent aquatic and terrestrial habitats. Species inhabiting these sterile environments are adapted to the abiotic conditions therein, but their prey choice is likely much less restricted, but almost certainly subject to the high variation of availability in prey from terrestrial and aquatic systems.

In this study, it was shown for the first time that larvae of water beetles of the family Haliplidae are potentially subsidizing the food-webs of small lake islands. Larvae of genera like *Haliplus* and *Peltodytes* feed on filamentous algae like *Spirogyra* spp. in lakes and ponds and crawl on land for their pupation in the soil (Beier 1929). In June, they reached high densities and sometimes > 100 larvae could be found in a single pitfall trap on the small islands of the Brüggehofsee. Also adult beetles of the genus *Haliplus* were frequently found in shore pitfall traps, predominantly in the Diersfordter Waldsee. However, their contribution to the diet of shore dwelling ground beetles and spiders remained unclear. Results of the stable isotope analysis show that *Haliplus confinis* and *Haliplus flavicollis* from the same habitats had highly separated niches. *H. flavicollis* had depleted  $\delta^{13}\text{C}$  signatures, typical for pelagic zooplankton feeders ( $-30 \pm 1.3 \text{ ‰}$ ), while *H. confinis* had the typically enriched  $\delta^{13}\text{C}$  signatures of benthic organisms ( $-22 \pm 2.2 \text{ ‰}$ ), but both species have nearly identical mean  $\delta^{15}\text{N}$  signatures of 4.0 ‰.

### Stoichiometry

The C:N ratios of ground beetles and spiders significantly differed, although there was some overlap between both arthropod groups. Beetles of the genus *Nebria* had significantly wider C:N ratios than other ground beetles and spiders. While ground beetles had higher relative carbon contents than spiders, spiders had higher relative nitrogen contents. Also ground beetles of the genus *Nebria* had higher relative carbon contents and lower relative nitrogen contents than other ground beetles. Additionally, ground beetles caught in August had usually wider C:N ratios than their conspecifics caught in June. C:N and N:P ratios are known to vary between ecosystems (Elser *et al.* 2000) and animal groups (Sterner & Elser 2002). The mean C:N ratios found in the present study are in good agreement with the values reported by Fagan and Denno (2004) for spiders and insect predators. They argue that spiders and insect predators in salt marshes might be nitrogen limited and more frequently feed on intraguild prey to compensate this limitation. Furthermore, spiders show a remarkably consistent pattern of C:N ratios across families and species, while ground beetles show much more variation in stoichiometry. Despite this constancy in C:N ratios, spiders and ground beetles had an extreme intraspecific variation in their relative carbon and nitrogen content. In contrast, the increased C:N ratios of ground beetles caught in August can be most likely attributed to increased lipid content. Ground beetles build up sufficient fat bodies in summer (July-August) either in reproductive tissues or lipid reserves for hibernation (Lovei & Sunderland 1996), so both stages of overwintering, larval or adult have higher fat contents in August/September. Surprisingly, also the *Nebria* spp. found in the study area were all autumn breeders, which overwinter as larvae (Thiele 1969; Telfer & Butterfield 2004), but in *N. livida*, C:N ratios seemingly decreased from June to August.

Since lipids are depleted in  $^{13}\text{C}$  following the fractionation during lipid synthesis in the step from pyruvate to acetyl coenzyme A (DeNiro & Epstein 1977),  $\delta^{13}\text{C}$  signatures of animals are known to vary with fat content. Animals with a higher proportion of lipids in body mass were found to have lower  $\delta^{13}\text{C}$  signatures (McConnaughey & McRoy 1979; Focken & Becker 1998). Thus, some studies performed lipid extraction prior to stable isotope analysis, to minimize the influence of the variation in fat content (e.g. Kling *et al.* 1992; Post *et al.* 2000a). However, it was found that lipid extraction also alters the  $\delta^{15}\text{N}$  signatures of animals (Sotiropoulos *et al.* 2004; Bodin *et al.* 2007), which is an undesirable effect in stable-isotope analysis of food-webs. It has therefore been proposed, to separate lipid extraction studies and later apply lipid corrections to stable-isotope analysis of food-webs, without altering  $\delta^{15}\text{N}$  (Sweeting *et al.* 2006). A number of studies found negative correlations of C:N to  $\delta^{13}\text{C}$  and used this relation for lipid correction models (Post *et al.* 2007; Logan *et al.* 2008; Mintenbeck *et al.* 2008). Most of these relationships were found for fish, but not always for aquatic invertebrates (Kiljunen *et al.* 2006). The relationship was also found to be weaker in terrestrial animals than in aquatic animals (Post *et al.* 2007).

Until today, no study has tested for a relationship between  $\delta^{13}\text{C}$  and C:N ratios in terrestrial arthropods. Nonetheless, some authors have removed body parts rich in lipids prior to stable isotope analysis to avoid biases in  $\delta^{13}\text{C}$  signature due to differing fat content of the target organisms (Hyodo & Wardle 2009; Mellbrand & Hambäck 2010).

In the present study, relations between C:N ratio and  $\delta^{13}\text{C}$  signature had high inter-specific variation. Relative carbon and nitrogen content increased with island area in the dominant spider species *P. prativaga* and *A. leopardus*. These patterns of variation point at nutritional constraints on smaller islands. But it seems unlikely that this increase in relative carbon and nitrogen content was related to increases in fat:protein ratios. Increases of fat:protein ratios with islands size would have lead to increases of C:N ratios with island size. In the present study no such relations between island size and C:N ratios were found. The decrease of  $\delta^{13}\text{C}$  signatures with island area thus is unlikely to be related to



changes in body fat content with island area and is more likely related to higher proportions of aquatic subsidies in the diet of spiders on small islands.

#### *Limits of the stable isotope approach*

It is a major drawback of mixing models and general assumptions about enrichment of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  in food webs that the food of a consumer is thought to be never enriched relative to this consumer. In other words, the poor spatial and temporal resolution of local food web models has led stable isotope analysis in ecology to the assumptions, that plants or prey cannot have a higher  $\delta^{15}\text{N}$  signature than their consumer. Supposedly, the  $\delta^{15}\text{N}$  signatures of organisms in a local food web are in line with their trophic positions. This very basic conception completely neglects the spatial variation of  $\delta^{15}\text{N}$  in soil and plants that even exist within a sampling location (Garten 1993; Woodcock *et al.* 2012) and most of all it neglects the spatial dynamics of species dispersal and foraging. The stable isotope analysis of the lake-island system in this study has shown that the spatial variation of  $\delta^{15}\text{N}$  in plants and consumers can span more than one trophic level, notably in regions with steep gradients of water availability and/or nitrification/denitrification processes. Additionally, common processes like vertebrate feces deposition can introduce a patchy distribution of contrasting  $\delta^{15}\text{N}$  signatures that translate into the  $\delta^{15}\text{N}$  signatures of primary producers and consumers in these local patches (Anderson & Polis 1999). The isotopic signatures of mobile predators colonizing such patches will react more slowly to these shifts in the isotopic signature of their prey (Gratton & Forbes 2006; Schallhart *et al.* 2009). Misinterpretation of consumer stable isotope signatures naturally follow, similar to misinterpretations due to temporal shift in baseline signatures (Matthews & Mazumder 2005). Intriguingly, this often neglected fact has been used to trace animal migration in other studies (Rubenstein & Hobson 2004). As a consequence, the interpretation of stable isotope results is scale dependent. The chance to reveal food web links and trophic positions of a particular species increases with the extent of the study area and sampling effort. This is a more derived result of the present study, since the local variation of food web interaction is visible from the stable isotope analysis of single islands, but predominant interactions become visible at the scale of the whole study. Considering this spatial variation is important for the method of choice used to explore food web dynamics and links and for choosing the right preconditions and assumptions for mixing models in stable isotope ecology. For instance, spiders recently have been found to feed more frequently on plant nectar than previously thought (Taylor & Pfannenstiel 2008). Accordingly, it has become tempting to incorporate plants into the mixing model of a spiders diet, but the consumption of plant nectar as suggested in such a model might be produced simply by the spatial variation in plant  $\delta^{15}\text{N}$ .

Scavenging can be seen as another serious problem in stable isotope analysis, for the consumption of dead arthropods by other insects cannot be distinguished from predation at all. This leads to an overestimation of predator prey interactions and false positives in identifying interactions in food webs (Wilson & Wolkovich 2011). Likewise, the contribution of scavenging to overall food web dynamics is usually neglected. Most notably, insect species adapted to predominantly feed on dead insects may be entirely overlooked in stable isotope studies. This is crucial for the understanding of predator- prey dynamics, since a pure scavenger does not increase the mortality of an assumed prey species and the scavenger might not directly compete with true predators for prey.

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## References

- Akamatsu F., Toda H. & Okino T. (2004). Food source of riparian spiders analyzed by using stable isotope ratios. *Ecological Research*, 19, 655-662.
- Akamatsu F., Toda H. & Okino T. (2007). Relating body size to the role of aquatic subsidies for the riparian spider *Nephila clavata*. *Ecological Research*, 22, 831-836.
- Al Hussein I.A. (2002). Occurrence and Habitat Selection of *Arctosa cinerea* (Fabr., 1777)(Araneae, Lycosidae) in Exhausted Opencast Brown Coal Mining Areas in Central Germany. *Archives of Nature Conservation & Landscape Research*, 41, 131-139.
- Allouche O., Kalyuzhny M., Moreno-Rueda G., Pizarro M. & Kadmon R. (2012). Area-heterogeneity tradeoff and the diversity of ecological communities. *Proceedings of the National Academy of Sciences*, 109, 17495-17500.
- Almqvist S. (1973). Spider associations in coastal sand dunes. *Oikos*, 24, 444-457.
- Anderson W. & Wait D. (2001). Subsidized island biogeography hypothesis: another new twist on an old theory. *Ecology Letters*, 4, 289-291.
- Anderson W.B. & Polis G.A. (1998). Marine Subsidies of Island Communities in the Gulf of California: Evidence from Stable Carbon and Nitrogen Isotopes. *Oikos*, 81, 75-80.
- Anderson W.B. & Polis G.A. (1999). Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. *Oecologia*, 118, 324-332.
- Arim M. & Marquet P.A. (2004). Intraguild predation: a widespread interaction related to species biology. *Ecology Letters*, 7, 557-564.
- Arrhenius O. (1921). Species and area. *Journal of Ecology*, 9, 95-99.
- Ås S. (1984). To fly or not to fly? Colonization of Baltic islands by winged and wingless carabid beetles. *Journal of Biogeography*, 11, 413-426.
- Ås S. (1993). Are habitat islands islands? Woodliving beetles (Coleoptera) in deciduous forest fragments in boreal forest. *Ecography*, 16, 219-228.
- Atmar W. & Patterson B.D. (1993). The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia*, 96, 373-755.
- Atmar W. & Patterson B.D. (1995). The nestedness temperature calculator: a visual basic program, including 294 presence-absence matrices. *AICS Research Incorporate and The Field Museum*.
- Aukema B. (1995). The evolutionary significance of wing dimorphism in carabid beetles (Coleoptera: Carabidae). *Researches on Population Ecology*, 37, 105-110.
- Barrett K., Anderson W.B., Wait D.A. & Grismer L.L. (2005). Marine subsidies alter the diet and abundance of insular and coastal lizard populations. *Oikos*, 109, 145-153.
- Barrett K., Wait D.A. & Anderson W.B. (2003). Small island biogeography in the Gulf of California: lizards, the subsidized island biogeography hypothesis, and the small island effect. *Journal of Biogeography*, 30, 1575-1581.
- Bartels P., Cucherousset J., Steger K., Eklöv P., Tranvik L.J. & Hillebrand H. (2012). Reciprocal subsidies between freshwater and terrestrial ecosystems structure consumer resource dynamics. *Ecology*, 93, 1173-1182.
- Bartrons M., Papes M., Diebel M., Gratton C. & Zanden M.J. (2013). Regional-Level Inputs of Emergent Aquatic Insects from Water to Land. *Ecosystems*, 16, 1353-1363.
- Bastow J.L., Sabo J.L., Finlay J.C. & Power M.E. (2002). A basal aquatic-terrestrial trophic link in rivers: algal subsidies via shore-dwelling grasshoppers. *Oecologia*, 131, 261-268.
- Baxter C.V., Fausch K.D. & Carl Saunders W. (2005). Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology*, 50, 201-220.
- Bayley P.B. (1995). Understanding large river: floodplain ecosystems. *BioScience*, 45, 153-158.
- Bearhop S., Adams C.E., Waldron S., Fuller R.A. & MacLeod H. (2004). Determining trophic niche width: a novel approach using stable isotope analysis. *Journal of Animal Ecology*, 73, 1007-1012.
- Becks L., Hilker F.M., Malchow H., Jürgens K. & Arndt H. (2005). Experimental demonstration of chaos in a microbial food web. *Nature*, 435, 1226-1229.

- Beier M. (1929). Zur Kenntnis der Lebensweise von *Haliplus wehnckei* Gerh. *Zoomorphology*, 14, 191-233.
- Bell G. (2001). Neutral macroecology. *Science*, 293, 2413-2418.
- Bell G. (2005). THE CO-DISTRIBUTION OF SPECIES IN RELATION TO THE NEUTRAL THEORY OF COMMUNITY ECOLOGY. *Ecology*, 86, 1757-1770.
- Bell J.R., Haughton A.J., Cullen W.R. & Wheater C.P. (1997). The zonation and ecology of a sand-dune spider community. In: *Proceedings of the 17th European Colloquium of Arachnology, Edinburgh*, pp. 261-266.
- Benincà E., Huisman J., Heerkloss R., Jöhnk K.D., Branco P., Van Nes E.H., Scheffer M. & Ellner S.P. (2008). Chaos in a long-term experiment with a plankton community. *Nature*, 451, 822-825.
- Berlow E.L. (1999). Strong effects of weak interactions in ecological communities. *Nature*, 398, 330-334.
- Bildstein K.L., Blood E. & Frederick P. (1992). The relative importance of biotic and abiotic vectors in nutrient transport. *Estuaries and Coasts*, 15, 147-157.
- Bodin N., Le Loc'h F.o. & Hily C. (2007). Effect of lipid removal on carbon and nitrogen stable isotope ratios in crustacean tissues. *Journal of Experimental Marine Biology and Ecology*, 341, 168-175.
- Boecklen W.J., Yarnes C.T., Cook B.A. & James A.C. (2011). On the use of stable isotopes in trophic ecology. *Annual Review of Ecology, Evolution, and Systematics*, 42, 411-440.
- Bonte D., Baert L., Lens L. & Maelfait J.P. (2004). Effects of aerial dispersal, habitat specialisation, and landscape structure on spider distribution across fragmented grey dunes. *Ecography*, 27, 343-349.
- Bonte D., Baert L. & Maelfait J.P. (2002). Spider assemblage structure and stability in a heterogeneous coastal dune system (Belgium). *Journal of Arachnology*, 30, 331-674.
- Brändle M., Durka W. & Altmöos M. (2000). Diversity of surface dwelling beetle assemblages in open-cast lignite mines in Central Germany. *Biodiversity & Conservation*, 9, 1297-1311.
- Briand F. (1983). Environmental control of food web structure. *Ecology*, 64, 253-263.
- Briand F. & Cohen J. (1987). Environmental correlates of food chain length. *Science (New York, N.Y.)*, 238, 956-1016.
- Briand F. & Cohen J.E. (1984). Community food webs have scale-invariant structure. *Nature*, 307, 264-267.
- Briers R.A., Cariss H.M., Geoghegan R. & Gee J.H. (2005). The lateral extent of the subsidy from an upland stream to riparian lycosid spiders. *Ecography*, 28, 165-170.
- Brose U. (2003). Island biogeography of temporary wetland carabid beetle communities. *Journal of Biogeography*, 30, 879-888.
- Brose U., Martinez N.D. & Williams R.J. (2003). Estimating species richness: sensitivity to sample coverage and insensitivity to spatial patterns. *Ecology*, 84, 2364-2377.
- Brose U., Williams R.J. & Martinez N.D. (2006). Allometric scaling enhances stability in complex food webs. *Ecology Letters*, 9, 1228-1236.
- Brotons L., Mönkkönen M. & Martin J. (2003). Are fragments islands? Landscape context and density-area relationships in boreal forest birds. *The American Naturalist*, 162, 343-400.
- Brown J.H. & Kodric-Brown A. (1977). Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology*, 58, 445-449.
- Brown J.H. & Lomolino M.V. (1989). Independent Discovery of the Equilibrium Theory of Island Biogeography. *Ecology*, 70, 1954-1957.
- Buckley R. & Kneidlhans S. (1986). Beachcomber biogeography: Interception of dispersing propagules by islands. *Journal of Biogeography*, 13, 69-70.
- Burns K.C., Paul McHardy R. & Pledger S. (2009). The small-island effect: fact or artefact? *Ecography*, 32, 269-276.
- Cadena C.D., Ricklefs R.E., Jimenez I. & Bermingham E. (2005). Ecology: Is speciation driven by species diversity? *Nature*, 438, E1-E2.
- Cadenasso M.L., Pickett S.T.A., Weathers K.C. & Jones C.G. (2003). A Framework for a Theory of Ecological Boundaries. *BioScience*, 53, 750-758.

- Cadotte M.W., Mai D.V., Jantz S., Collins M.D., Keele M. & Drake J.A. (2006). On Testing the Competition-Colonization Trade-Off in a Multispecies Assemblage. *The American Naturalist*, 168, 704-709.
- Camin J.H. & Ehrlich P.R. (1958). Natural selection in water snakes (*Natrix sipedon* L.) on islands in Lake Erie. *Evolution*, 12, 504-511.
- Carpenter S., Kitchell J., Hodgson J., Cochran P., Elser J., Elser M., Lodge D., Kretchmer D., He X. & Von Ende C. (1987). Regulation of lake primary productivity by food web structure. *Ecology*, 68, 1863-1876.
- Carpenter S.R., Cole J.J., Pace M.L., Van de Bogert M., Bade D.L., Bastviken D., Gille C.M., Hodgson J.R., Kitchell J.F. & Kritzberg E.S. (2005). Ecosystem subsidies: terrestrial support of aquatic food webs from <sup>13</sup>C addition to contrasting lakes. *Ecology*, 86, 2737-2750.
- Caut S., Angulo E., Pisanu B., Ruffino L., Faulquier L., Lorvelec O., Chapuis J.-L., Pascal M., Vidal E. & Courchamp F. (2012). Seabird modulations of isotopic nitrogen on islands. *PLoS ONE*, 7, e39125.
- Chase J.M. (2000). Are there real differences among aquatic and terrestrial food webs? *Trends in ecology & evolution*, 15, 408-412.
- Cheney K.L. & Côté I.M. (2005). Mutualism or parasitism? The variable outcome of cleaning symbioses. *Biology Letters*, 1, 162-165.
- Chesson P., Gebauer R.L.E., Schwinning S., Huntly N., Wiegand K., Ernest M.S.K., Sher A., Novoplansky A. & Waltzin J.F. (2004). Resource Pulses, Species Interactions, and Diversity Maintenance in Arid and Semi-Arid Environments. *Oecologia*, 141, 236-253.
- Clarke K.R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, 18, 117-143.
- Clements F.E. (1916). *Plant succession : an analysis of the development of vegetation*. Carnegie Institution of Washington, Washington.
- Cloern J.E., Canuel E.A. & Harris D. (2002). Stable carbon and nitrogen isotope composition of aquatic and terrestrial plants of the San Francisco Bay estuarine system. *Limnology and Oceanography*, 47, 713-729.
- Cohen J.E. & Briand F. (1984). Trophic links of community food webs. *Proceedings of the National Academy of Sciences*, 81, 4105-4109.
- Cohen J.E. & Newman C.M. (1991). Community area and food-chain length: theoretical predictions. *American Naturalist*, 138, 1542-1554.
- Colebourn P. (1974). The influence of habitat structure on the distribution of *Araneus diadematus* Clerck. *The Journal of Animal Ecology*, 43, 401-409.
- Coll M. & Guershon M. (2002). Omnivory in terrestrial arthropods: mixing plant and prey diets. *Annual Review of Entomology*, 47, 267-297.
- Collier K.J., Bury S. & Gibbs M. (2002). A stable isotope study of linkages between stream and terrestrial food webs through spider predation. *Freshwater Biology*, 47, 1651-1659.
- Connor E.F., Courtney A.C. & Yoder J.M. (2000). Individuals-area relationships: the relationship between animal population density and area. *Ecology*, 81, 734-1482.
- Connor E.F. & McCoy E.D. (1979). The statistics and biology of the species-area relationship. *The American Naturalist*, 113, 791-1624.
- Cook W.M., Lane K.T., Foster B.L. & Holt R.D. (2002). Island theory, matrix effects and species richness patterns in habitat fragments. *Ecology Letters*, 5, 619-623.
- Cyr H. & Pace M.L. (1993). Magnitude and patterns of herbivory in aquatic and terrestrial ecosystems. *Nature*, 361, 148-150.
- Darlington P. (1943). Carabidae of mountains and islands: data on the evolution of isolated faunas, and on atrophy of wings. *Ecological Monographs*, 13, 37-61.
- Darnell R.M. (1961). Trophic spectrum of an estuarine community, based on studies of Lake Pontchartrain, Louisiana. *Ecology*, 42, 553-568.
- de Ruiter P.C., Neutel A.-M. & Moore J.C. (1995). Energetics, Patterns of Interaction Strengths, and Stability in Real Ecosystems. *Science*, 269, 1257-1260.
- Debinski D.M. & Holt R.D. (2000). A survey and overview of habitat fragmentation experiments. *Conservation Biology*, 14, 342-355.
- den Boer P. (1990). Density limits and survival of local populations in 64 carabid species with different powers of dispersal. *Journal of Evolutionary Biology*, 3, 19-48.

- den Boer P.J. (1970). On the Significance of Dispersal Power for Populations of Carabid-Beetles (Coleoptera, Carabidae). *Oecologia*, 4, 1-28.
- Dengler J.r. (2010). Robust methods for detecting a small island effect. *Diversity and Distributions*, 16, 256-266.
- DeNiro M. & Epstein S. (1977). Mechanism of carbon isotope fractionation associated with lipid synthesis. *Science*, 197, 261-263.
- DeNiro M.J. & Epstein S. (1978). Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta*, 42, 495-506.
- Deniro M.J. & Epstein S. (1981). Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta*, 45, 341-351.
- Desender K. (1989). Heritability of wing development and body size in a carabid beetle, *Pogonus chalceus* MARSHAM, and its evolutionary significance. *Oecologia*, 78, 513-520.
- Diamond J. (1975a). Assembly of species communities. In: Cody, ML and Diamond, JM (eds), Ecology and evolution of communities. In: Harvard Univ. Press, pp. 342.
- Diamond J.M. (1975b). The island dilemma: Lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation*, 7, 129-146.
- Dodds W.K. (2006). Eutrophication and trophic state in rivers and streams. *Limnology and Oceanography*, 51, 671-680.
- Doi H., Chang K.-H., Ando T., Ninomiya I., Imai H. & Nakano S.-i. (2009). Resource availability and ecosystem size predict food-chain length in pond ecosystems. *Oikos*, 118, 138-144.
- Doi H., Kikuchi E., Shikano S. & Takagi S. (2010). Differences in nitrogen and carbon stable isotopes between planktonic and benthic microalgae. *Limnology*, 11, 185-192.
- Douglas M. & Lake P.S. (1994). Species Richness of Stream Stones: An Investigation of the Mechanisms Generating the Species-Area Relationship. *Oikos*, 69, 387-396.
- Dreyer J., Hoekman D. & Gratton C. (2012). Lake-derived midges increase abundance of shoreline terrestrial arthropods via multiple trophic pathways. *Oikos*, 121, 252-258.
- Dunne J., Williams R. & Martinez N. (2002). Food-web structure and network theory: The role of connectance and size. *Proceedings of the National Academy of Sciences of the United States of America*, 99, 12917-12939.
- Elser J.J., Fagan W.F., Denno R.F., Dobberfuhl D.R., Folarin A., Huberty A., Interlandi S., Kilham S.S., McCauley E. & Schulz K.L. (2000). Nutritional constraints in terrestrial and freshwater food webs. *Nature*, 408, 578-580.
- Elton C.S. (1927). *Animal ecology*. University of Chicago Press.
- Emerson B.C. & Kolm N. (2005). Species diversity can drive speciation. *Nature*, 434, 1015-1017.
- Emmerson M.C. & Raffaelli D. (2004). Predator-prey body size, interaction strength and the stability of a real food web. *Journal of Animal Ecology*, 73, 399-409.
- Entling W., Schmidt M.H., Bacher S., Brandl R. & Nentwig W. (2007). Niche properties of Central European spiders: shading, moisture and the evolution of the habitat niche. *Global Ecology and Biogeography*, 16, 440-448.
- Estes J.A., Terborgh J., Brashares J.S., Power M.E., Berger J., Bond W.J., Carpenter S.R., Essington T.E., Holt R.D. & Jackson J.B. (2011). Trophic downgrading of planet earth. *Science*, 333, 301-306.
- Fabricius K.E. (2005). Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Marine pollution bulletin*, 50, 125-146.
- Fagan W.F. & Denno R.F. (2004). Stoichiometry of actual vs. potential predator-prey interactions: insights into nitrogen limitation for arthropod predators. *Ecology Letters*, 7, 876-883.
- Fleming T.H. & Muchhala N. (2008). Nectar-feeding bird and bat niches in two worlds: pantropical comparisons of vertebrate pollination systems. *Journal of Biogeography*, 35, 764-780.
- Fletcher J.R.J., Ries L., Battin J. & Chalfoun A.D. (2007). The role of habitat area and edge in fragmented landscapes: definitively distinct or inevitably intertwined? *Canadian Journal of Zoology*, 85, 1017-1030.
- Focken U. & Becker K. (1998). Metabolic fractionation of stable carbon isotopes: implications of different proximate compositions for studies of the aquatic food webs using  $\delta^{13}\text{C}$  data. *Oecologia*, 115, 337-343.
- Fox L.R. (1975). Cannibalism in Natural Populations. *Annual Review of Ecology and Systematics*, 6, 87-106.

- France R.L. (1995). Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. *Marine Ecology Progress Series*, 124, 307-312.
- Fretwell S.D. (1977). The regulation of plant communities by food chains exploiting them. *Perspectives in Biology and Medicine*, 20, 85.
- Freude H., Harde K.W., Lohse G.A. & Klausnitzer B. (2006). Bd.2 Adephaga 1: Carabidae (Laufkäfer). In: *Die Käfer Mitteleuropas* (ed. Müller-Motzfeld G). Spektrum Verlag Heidelberg/Berlin.
- Freyer H. (1978). Seasonal trends of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  nitrogen isotope composition in rain collected at Jülich, Germany. *Tellus*, 30, 83-92.
- Freyer H. (1991). Seasonal variation of  $^{15}\text{N}/^{14}\text{N}$  ratios in atmospheric nitrate species. *Tellus B*, 43, 30-44.
- Fukami T. (2004). Assembly history interacts with ecosystem size to influence species diversity. *Ecology*, 85, 3234-6476.
- Furnas M.J. (2003). Catchments and corals: terrestrial runoff to the Great Barrier Reef. *Australian Institute of Marine Science & CRC Reef Research Centre*, 334.
- Gack C., Kobel-Lamparski A. & Lamparski F. (1999). Spider communities as indicators of the development (succession) of afforested coal mining sites. *Arachnologische Mitteilungen*, 18, 1-16.
- Gagnon A.-É., Heimpel G.E. & Brodeur J. (2011). The ubiquity of intraguild predation among predatory arthropods. *PLoS ONE*, 6, e28061.
- Garlaschelli D., Caldarelli G. & Pietronero L. (2003). Universal scaling relations in food webs. *Nature*, 423, 165-168.
- Garten C.T. (1993). Variation in Foliar  $^{15}\text{N}$  Abundance and the Availability of Soil Nitrogen on Walker Branch Watershed. *Ecology*, 74, 2098-2113.
- Gilpin M.E. & Armstrong R.A. (1981). On the concavity of island biogeographic rate functions. *Theoretical Population Biology*, 20, 209-217.
- Gotelli N. & Entsminger G. (2009). EcoSim: Null models software for ecology. Version 7. Acquired Intelligence Inc. & Kesey-Bear. Jericho, VT 05465. In.
- Gotelli N.J. & Entsminger G.L. (2003). Swap algorithms in null model analysis. *Ecology*, 84, 532-1067.
- Gotelli N.J. & McCabe D.J. (2002). Species co-occurrence: a meta-analysis of JM Diamond's assembly rules model. *Ecology*, 83, 2091-4187.
- Gratton C. & Forbes A.E. (2006). Changes in  $\delta^{13}\text{C}$  stable isotopes in multiple tissues of insect predators fed isotopically distinct prey. *Oecologia*, 147, 615-624.
- Gratton C. & VanderZanden M.J. (2009). Flux of aquatic insect productivity to land: comparison of lentic and lotic ecosystems. *Ecology*, 90, 2689-2699.
- Gröning J., Kochmann J. & Hochkirch A. (2005). Ground-hoppers (Orthoptera, Tetrigidae) on the East Frisian Islands (Germany, Lower Saxony), with notes on their distribution, coexistence and ecology. *Entomol Heute*, 17, 47-63.
- Gröning J., Krause S. & Hochkirch A. (2007). Habitat preferences of an endangered insect species, Cepero's ground-hopper (*Tetrix ceperoi*). *Ecological Research*, 22, 767-773.
- Gutiérrez D. & Menéndez R. (1997). Patterns in the distribution, abundance and body size of carabid beetles (Coleoptera: Caraboidea) in relation to dispersal ability. *Journal of Biogeography*, 24, 903-914.
- Hairston J., Nelson G & Hairston S., Nelson G (1997). Does food web complexity eliminate trophic-level dynamics? *The American Naturalist*, 149, 1001-1007.
- Hairston N.G., Smith F.E. & Slobodkin L.B. (1960). Community structure, population control, and competition. *American naturalist*, 94, 421-425.
- Hammer O., Harper D.A. & Ryan P.D. (2001). PAST-Palaeontological statistics. <http://folk.uio.no/ohammer/past/>, 14, 2014.
- Handley L.L., Austin A.T., Stewart G.R., Robinson D., Scrimgeour C.M., Raven J.A., Heaton T.H.E. & Schmidt S. (1999). The  $^{15}\text{N}$  natural abundance ( $\delta^{15}\text{N}$ ) of ecosystem samples reflects measures of water availability. *Functional Plant Biology*, 26, 185-199.
- Hanski I. (1998). Metapopulation dynamics. *Nature*, 396, 41-49.
- Hanski I. & Gilpin M. (1991). Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society*, 42, 3-16.

- Harris D., Horwath W.R. & van Kessel C. (2001). Acid fumigation of soils to remove carbonates prior to total organic carbon or CARBON-13 isotopic analysis. *Soil Sci. Soc. Am. J.*, 65, 1853-1856.
- Hartman G. & Danin A. (2010). Isotopic values of plants in relation to water availability in the Eastern Mediterranean region. *Oecologia*, 162, 837-852.
- Hastings A. & Powell T. (1991). Chaos in a three-species food chain. *Ecology*, 896-903.
- Havik G., Catenazzi A. & Holmgren M. (2014). Seabird Nutrient Subsidies Benefit Non-Nitrogen Fixing Trees and Alter Species Composition in South American Coastal Dry Forests. *PLoS ONE*, 9, e86381.
- Heaney L.R. (2000). Dynamic disequilibrium: a long-term, large-scale perspective on the equilibrium model of island biogeography. *Global Ecology and Biogeography*, 9, 59-74.
- Hecky R. & Hesslein R. (1995). Contributions of benthic algae to lake food webs as revealed by stable isotope analysis. *Journal of the North American Benthological Society*, 14, 631-653.
- Heil M. & McKey D. (2003). Protective Ant-Plant Interactions as Model Systems in Ecological and Evolutionary Research. *Annual Review of Ecology, Evolution, and Systematics*, 34, 425-453.
- Henschel J.R., Mahsberg D. & Stumpf H. (2001). Allochthonous aquatic insects increase predation and decrease herbivory in river shore food webs. *Oikos*, 93, 429-438.
- Hobson K.A. (1999). Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia*, 120, 314-326.
- Hoekman D., Dreyer J., Jackson R.D., Townsend P.A. & Gratton C. (2011). Lake to land subsidies: experimental addition of aquatic insects increases terrestrial arthropod densities. *Ecology*, 92, 2063-2072.
- Holeski P.M. (1984). Possible colonization strategies of some carabid beetles inhabiting stream shores (Coleoptera: Carabidae). *Great Lakes Entomologist*, 17, 1-8.
- Holt R.D. (1985). Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. *Theoretical Population Biology*, 28, 181-208.
- Holt R.D. (1993). Ecology at the mesoscale: the influence of regional processes on local communities. In: *Species diversity in ecological communities* (eds. Ricklefs RE & Schluter D). University of Chicago Press Chicago, pp. 77-88.
- Holt R.D. (2002). Food webs in space: On the interplay of dynamic instability and spatial processes. *Ecological Research*, 17, 261-273.
- Holt R.D. (2008). Theoretical perspectives on resource pulses. *Ecology*, 89, 671-681.
- Holt R.D. & Hoopes M.F. (2005). Food web dynamics in a metacommunity context. In: *Metacommunities: spatial dynamics and ecological communities* (eds. Holyoak M, Leibold MA & Holt RD). The University of Chicago Press Chicago and London, pp. 68-93.
- Holt R.D., Losos J. & Ricklefs R. (2009). Toward a trophic island biogeography. In: *The theory of island biogeography revisited* (eds. Losos JB & Ricklefs RE). Princeton University Press, p. 143.
- Holyoak M., Leibold M.A. & Holt R.D. (2005). *Metacommunities: spatial dynamics and ecological communities*. University of Chicago Press, Chicago and London.
- Hortal J., Borges P.A. & Gaspar C. (2006). Evaluating the performance of species richness estimators: sensitivity to sample grain size. *Journal of Animal Ecology*, 75, 274-287.
- Howe H. & Smallwood J. (1982). Ecology of Seed Dispersal. *Annual Review of Ecology and Systematics*, 13, 201-228.
- Hubbell S.P. (2001). *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, N.J. [etc.].
- Hurka K. & Jarosik V. (2003). Larval omnivory in *Amara aenea* (Coleoptera: Carabidae). *European Journal of Entomology*, 100, 329-336.
- Hutchinson G.E. (1959). Homage to Santa Rosalia or why are there so many kinds of animals? *American naturalist*, 93, 145-159.
- Hutchinson G.E. (1991). Population studies: Animal ecology and demography. *Bulletin of Mathematical Biology*, 53, 193-213.
- Hyodo F. & Wardle D.A. (2009). Effect of ecosystem retrogression on stable nitrogen and carbon isotopes of plants, soils and consumer organisms in boreal forest islands. *Rapid Communications in Mass Spectrometry*, 23, 1892-1898.
- Ings T., Montoya J., Bascompte J., Blüthgen N., Brown L., Dormann C., Edwards F., Figueroa D., Jacob U., Jones J., Lauridsen R., Ledger M., Lewis H., Olesen J., van Veen F., Warren P. &



- Woodward G. (2009). Ecological networks--beyond food webs. *The Journal of Animal Ecology*, 78, 253-269.
- Irmeler U. (2003). The spatial and temporal pattern of carabid beetles on arable fields in northern Germany (Schleswig-Holstein) and their value as ecological indicators. *Agriculture, Ecosystems & Environment*, 98, 141-151.
- Jaccard P. (1912). The distribution of the flora in the alpine zone. *New Phytologist*, 11, 37-87.
- Jackson A.L., Inger R., Parnell A.C. & Bearhop S. (2011). Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology*, 80, 595-602.
- Jackson J.K. & Fisher S.G. (1986). Secondary Production, Emergence, and Export of Aquatic Insects of a Sonoran Desert Stream. *Ecology*, 67, 629-638.
- Jansson M., Persson L., De Roos A.M., Jones R.I. & Tranvik L.J. (2007). Terrestrial carbon and intraspecific size-variation shape lake ecosystems. *Trends in Ecology & Evolution*, 22, 316-322.
- Jefferies R., Rockwell R. & Abraham K. (2004). Agricultural food subsidies, migratory connectivity and large-scale disturbance in arctic coastal systems: a case study. *Integrative and Comparative Biology*, 44, 130-139.
- Jenkins B., Kitching R. & Pimm S. (1992). Productivity, disturbance and food web structure at a local spatial scale in experimental container habitats. *Oikos*, 65, 249-255.
- Jensen K., Mayntz D., Toft S.r., Raubenheimer D. & Simpson S. (2011). Prey nutrient composition has different effects on *Pardosa wolf* spiders with dissimilar life histories. *Oecologia*, 165, 577-583.
- Jonsson M. & Wardle D.A. (2009). The influence of freshwater-lake subsidies on invertebrates occupying terrestrial vegetation. *Acta Oecologica*, 35, 698-704.
- Kallimanis A.S., Mazaris A.D., Tzanopoulos J., Halley J.M., Pantis J.D. & Sgardelis S.P. (2008). How does habitat diversity affect the species-area relationship? *Global Ecology and Biogeography*, 17, 532-538.
- Karlsson J., Byström P., Ask J., Ask P., Persson L. & Jansson M. (2009). Light limitation of nutrient-poor lake ecosystems. *Nature*, 460, 506-509.
- Kato C., Iwata T., Nakano S. & Kishi D. (2003). Dynamics of aquatic insect flux affects distribution of riparian web-building spiders. *Oikos*, 103, 113-120.
- Kato C., Iwata T. & Wada E. (2004). Prey use by web-building spiders: stable isotope analyses of trophic flow at a forest-stream ecotone. *Ecological Research*, 19, 633-643.
- Kaunzinger C.M. & Morin P.J. (1998). Productivity controls food-chain properties in microbial communities. *Nature*, 395, 495-497.
- Kavanaugh D.H. (1985). On wing atrophy in carabid beetles (Coleoptera: Carabidae), with special reference to Nearctic *Nebria*. In: *Taxonomy, phylogeny and zoogeography of beetles and ants* (ed. Ball GE). Dr. W Junk Publishers Dordrecht, pp. 408-431.
- Kier G., Kreft H., Lee T.M., Jetz W., Ibsch P.L., Nowicki C., Mutke J. & Barthlott W. (2009). A global assessment of endemism and species richness across island and mainland regions. *Proceedings of the National Academy of Sciences*, 106, 9322-9327.
- Kiljunen M., Grey J., Sinisalo T., Harrod C., Immonen H. & Jones R.I. (2006). A revised model for lipid-normalizing  $\delta^{13}\text{C}$  values from aquatic organisms, with implications for isotope mixing models. *Journal of Applied Ecology*, 43, 1213-1222.
- King R.A., Read D.S., Traugott M. & Symondson W.O.C. (2008). Molecular analysis of predation: a review of best practice for DNA-based approaches. *Molecular Ecology*, 17, 947-963.
- Kling G.W., Fry B. & O'Brien W.J. (1992). Stable isotopes and planktonic trophic structure in arctic lakes. *Ecology*, 73, 561-566.
- Knight T.M., McCoy M.W., Chase J.M., McCoy K.A. & Holt R.D. (2005). Trophic cascades across ecosystems. *Nature*, 437, 880-883.
- Kohn D.D. & Walsh D.M. (1994). Plant Species Richness--The Effect of Island Size and Habitat Diversity. *The Journal of Ecology*, 82, 367-377.
- Kolb G.S., Jerling L., Essenberg C., Palmberg C. & Hambäck P.A. (2012). The impact of nesting cormorants on plant and arthropod diversity. *Ecography*, 35, 726-740.
- Komonen A., Penttilä R., Lindgren M. & Hanski I. (2000). Forest fragmentation truncates a food chain based on an old growth forest bracket fungus. *Oikos*, 90, 119-245.

- Kotze D.J. & Niemelä J. (2002a). Year-to-year variation in carabid beetle (Coleoptera, Carabidae) assemblages on the Åland Islands, south-west Finland. *Journal of Biogeography*, 29, 375-386.
- Kotze D.J. & Niemelä J. (2002b). Year-to-year variation in carabid beetle (Coleoptera, Carabidae) assemblages on the Åland Islands, south-west Finland. *Journal of Biogeography*, 29, 375-386.
- Kotze D.J., Niemelä J. & Nieminen M. (2000). Colonization success of carabid beetles on Baltic islands. *Journal of Biogeography*, 27, 807-819.
- Kozlovsky D.G. (1968). A critical evaluation of the trophic level concept. I. Ecological efficiencies. *Ecology*, 48-60.
- Krause A., Frank K., Mason D., Ulanowicz R. & Taylor W. (2003). Compartments revealed in food-web structure. *Nature*, 426, 282-287.
- Krauss J., Steffan-Dewenter I. & Tschardt T. (2003). Local species immigration, extinction, and turnover of butterflies in relation to habitat area and habitat isolation. *Oecologia*, 137, 591-602.
- Kruess A. & Tschardt T. (2000). Species richness and parasitism in a fragmented landscape: experiments and field studies with insects on *Vicia sepium*. *Oecologia*, 122, 129-137.
- Lajtha K. & Marshall J. (1994). Sources of variation in isotopic composition in plants. *Stable isotopes in ecological and environmental sciences*. Oxford University Press, London, 1-21.
- Lajtha K. & Michener R. (1994). *Stable isotopes in ecology and environmental science*. Oxford University Press, London.
- Lambeets K., Bonte D., Van Looy K., Hendrickx F. & Maelfait J.P. (2005). Synecology of spiders (Araneae) of gravel banks and environmental constraints along a lowland river system, the Common Meuse (Belgium, the Netherlands). *Acta zoologica bulgarica*, 1, 137-149.
- Lambeets K., Hendrickx F., Vanacker S., Van Looy K., Maelfait J.-P. & Bonte D. (2008). Assemblage structure and conservation value of spiders and carabid beetles from restored lowland river banks. *Biodiversity and Conservation*, 17, 3133-3148.
- Lancaster J., Dobson M., Magana A.M., Arnold A. & Mathooko J.M. (2008). An unusual trophic subsidy and species dominance in a tropical stream. *Ecology*, 89, 2325-2334.
- Laska M.S. & Wootton J.T. (1998). Theoretical concepts and empirical approaches to measuring interaction strength. *Ecology*, 79, 461-476.
- Lawton J.H. (1999). Are there general laws in ecology? *Oikos*, 84, 177-192.
- Layman C.A., Arrington D.A., Montoya C.G. & Post D.M. (2007). Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology*, 88, 42-48.
- Lehmann H. (1965). Ökologische Untersuchungen über die Carabidenfauna des Rheinuferes in der Umgebung von Köln. *Zoomorphology*, 55, 597-630.
- Leibold M.A., Holyoak M., Mouquet N., Amarasekare P., Chase J., Hoopes M., Holt R., Shurin J., Law R. & Tilman D. (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, 7, 601-613.
- Leroux S. & Loreau M. (2012). Dynamics of Reciprocal Pulsed Subsidies in Local and Meta-Ecosystems. *Ecosystems*, 15, 48-59.
- Li H. & Reynolds J.F. (1995). On Definition and Quantification of Heterogeneity. *Oikos*, 73, 280-284.
- Likens G.E. & Bormann F.H. (1974). Linkages between terrestrial and aquatic ecosystems. *BioScience*, 24, 447-456.
- Lindeman R.L. (1942). The trophic-dynamic aspect of ecology. *Ecology*, 23, 399-417.
- Logan J., Jardine T., Miller T., Bunn S., Cunjak R. & Lutcavage M. (2008). Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical extraction and modelling methods. *The Journal of Animal Ecology*, 77, 838-846.
- Lomolino M. & Weiser M. (2001). Towards a more general species-area relationship: diversity on all islands, great and small. *Journal of Biogeography*, 28, 431-876.
- Lomolino M.V. (1990). The target area hypothesis: the influence of island area on immigration rates of non-volant mammals. *Oikos*, 297-300.
- Loreau M., Mouquet N. & Holt R.D. (2003). Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. *Ecology Letters*, 6, 673-679.
- Losos J.B. & Ricklefs R.E. (2009). *The theory of island biogeography revisited*. Princeton University Press.
- Lovei G.L. & Sunderland K.D. (1996). Ecology and behavior of ground beetles (Coleoptera: Carabidae). *Annual Review of Entomology*, 41, 231-256.

- Luff M.L. (1998). *Provisional atlas of the ground beetles (Coleoptera, Carabidae) of Britain*. Biological Records Centre Institute of Terrestrial Ecology.
- MacArthur R.H. & Wilson E.O. (1963). An equilibrium theory of insular zoogeography. *Evolution*, 373-387.
- MacArthur R.H. & Wilson E.O. (1967). *The theory of island biogeography*. Princeton University Press.
- Marczak L., Thompson R. & Richardson J. (2007). Meta-analysis: trophic level, habitat, and productivity shape the food web effects of resource subsidies. *Ecology*, 88, 140-148.
- Marczak L.B. & Richardson J.S. (2007). Spiders and subsidies: results from the riparian zone of a coastal temperate rainforest. *Journal of Animal Ecology*, 76, 687-694.
- Martinez N.D. (1992). Constant connectance in community food webs. *American naturalist*, 139, 1208-1218.
- Martinez N.D. (1994). Scale-dependent constraints on food-web structure. *American naturalist*, 144, 935-953.
- Matthews B. & Mazumder A. (2005). Consequences of large temporal variability of zooplankton  $\delta^{15}\text{N}$  for modeling fish trophic position and variation. *Limnology and Oceanography*, 50, 1404.
- May R.M. (1973). Qualitative Stability in Model Ecosystems. *Ecology*, 54, 638-641.
- McCann K., Hastings A. & Huxel G.R. (1998). Weak trophic interactions and the balance of nature. *Nature*, 395, 794-798.
- McConnaughey T. & McRoy C.P. (1979). Food-Web structure and the fractionation of Carbon isotopes in the bering sea. *Marine Biology*, 53, 257-262.
- McCoy M.W., Barfield M. & Holt R.D. (2009). Predator shadows: complex life histories as generators of spatially patterned indirect interactions across ecosystems. *Oikos*, 118, 87-100.
- McCutchan J.H., Lewis W.M., Kendall C. & McGrath C.C. (2003). Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos*, 102, 378-390.
- McHugh P.A., McIntosh A.R. & Jellyman P.G. (2010). Dual influences of ecosystem size and disturbance on food chain length in streams. *Ecology Letters*, 13, 881-890.
- Meijer J. (1974). A comparative study of the immigration of carabids (Coleoptera, Carabidae) into a new polder. *Oecologia*, 16, 185-393.
- Mellbrand K. (2009). The spider and the sea: effects of marine subsidies on the role of spiders in terrestrial food webs. In: *Doctoral thesis; Department of Botany*. Stockholm University Stockholm, p. 44.
- Mellbrand K. & Hambäck P.A. (2010). Coastal niches for terrestrial predators: a stable isotope study. *Canadian Journal of Zoology*, 88, 1077-1085.
- Mellbrand K., Lavery P.S., Hyndes G. & Hambäck P.A. (2011). Linking land and sea: different pathways for marine subsidies. *Ecosystems*, 14, 732-744.
- Miller T.E. & Kneitel J.M. (2005). Inquiline communities in pitcher plants as a prototypical metacommunity. In: *Metacommunities: spatial dynamics and ecological communities* (eds. Holyoak M, Leibold MA & Holt RD). University of Chicago Press Chicago and London, p. 145.
- Minagawa M. & Wada E. (1984). Stepwise enrichment of  $^{15}\text{N}$  along food chains: Further evidence and the relation between  $[\delta^{15}\text{N}]$  and animal age. *Geochimica et Cosmochimica Acta*, 48, 1135-2275.
- Mintenbeck K., Brey T., Jacob U., Knust R. & Struck U. (2008). How to account for the lipid effect on carbon stable isotope ratio ( $\delta^{13}\text{C}$ ): sample treatment effects and model bias. *Journal of Fish Biology*, 72, 815-830.
- Morrison L.W. (2002). Determinants of plant species richness on small Bahamian islands. *Journal of Biogeography*, 29, 931-941.
- Mouquet N. & Loreau M. (2003). Community patterns in source-sink metacommunities. *The American Naturalist*, 162, 544-601.
- Muehlbauer J.D., Collins S.F., Doyle M.W. & Tockner K. (2014). How wide is a stream? Spatial extent of the potential "stream signature" in terrestrial food webs using meta-analysis. *Ecology*, 95, 44-55.
- Munroe E. (1953). The size of island faunas. In: *Proceedings of the Seventh Pacific Science Congress of the Pacific Science Association*, pp. 52-53.

- Murakami M. & Nakano S. (2002). Indirect effect of aquatic insect emergence on a terrestrial insect population through by birds predation. *Ecology Letters*, 5, 333-337.
- Murray B.R., Rice B.L., Keith D.A., Myerscough P.J., Howell J., Floyd A.G., Mills K. & Westoby M. (1999). Species in the tail of rank-abundance curves. *Ecology*, 80, 1806-1816.
- Nakano S., Miyasaka H. & Kuhara N. (1999). Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. *Ecology*, 80, 2435-2441.
- Nentwig W., Hänggi A., Kropf C. & Blick T. (2003). Spinnen Mitteleuropas/Central European Spiders. An internet identification key. In. Version 6.2011 [www.araneae.unibe.ch](http://www.araneae.unibe.ch).
- Neumann U. (1971). *Die sukzession der bodenfauna (Carabidae [Coleoptera], Diplopoda und Isopoda) in den forstlich rekultivierten Gebieten des Rheinischen Braunkohlenreviers*. Gustav Fischer Verlag.
- Neutel A.-M., Heesterbeek J.A. & de Ruiter P.C. (2002). Stability in real food webs: weak links in long loops. *Science*, 296, 1120-1123.
- Neutel A.-M., Heesterbeek J.A., van de Koppel J., Hoenderboom G., Vos A., Kaldeway C., Berendse F. & de Ruiter P.C. (2007). Reconciling complexity with stability in naturally assembling food webs. *Nature*, 449, 599-602.
- Newsome S.D., Martinez del Rio C., Bearhop S. & Phillips D.L. (2007). A niche for isotopic ecology. *Frontiers in Ecology and the Environment*, 5, 429-436.
- Niemelä J., Haila Y. & Halme E. (1988). Carabid beetles on isolated Baltic islands and on the adjacent Aaland mainland: Variation in colonization success. *Annales Zoologici Fennici*, 25, 133-276.
- Niemelä J., Haila Y., Ranta E., Tiainen J., Vepsäläinen K. & Ås S. (1987). Distribution of carabid beetles in four boreal archipelagoes. *Annales Zoologici Fennici*, 24, 89-100.
- Niemelä J. & Spence J.R. (1999). Dynamics of local expansion by an introduced species: *Pterostichus melanarius* Ill. (Coleoptera, Carabidae) in Alberta, Canada. *Diversity and Distributions*, 5, 121-127.
- Niering W.A. (1963). Terrestrial ecology of Kapingamarangi Atoll, Caroline Islands. *Ecological Monographs*, 33, 131-160.
- Nowlin W.H., González M.a.J., Vanni M.J., Stevens M.H.H., Fields M.W. & Valente J.J. (2007). Allochthonous subsidy of periodical cicadas affects the dynamics and stability of pond communities. *Ecology*, 88, 2174-2186.
- O'Neill R.V. (2001). Is it time to bury the ecosystem concept? (With full military honours of course!) *Ecology*, 82, 3275-3284.
- O'Reilly C.M., Hecky R.E., Cohen A.S. & Plisnier P.D. (2002). Interpreting Stable Isotopes in Food Webs: Recognizing the Role of Time Averaging at Different Trophic Levels. *Limnology and Oceanography*, 47, 306-309.
- Odum H.T. (1957). Trophic structure and productivity of Silver Springs, Florida. *Ecological Monographs*, 27, 55-112.
- Odum H.T. & Odum E.P. (1955). Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. *Ecological Monographs*, 25, 291-320.
- Oksanen J., Blanchet F.G., Kindt R., Legendre P., Minchin P.R., O'Hara R., Simpson G.L., Oksanen M.J. & Suggests M. (2013). Package 'vegan'. Accesible via: <http://cran.r-project.org/web/packages/vegan/index.html>.
- Oksanen L., Fretwell S.D., Arruda J. & Niemela P. (1981). Exploitation ecosystems in gradients of primary productivity. *American naturalist*, 118, 240-261.
- Pace M.L., Cole J.J., Carpenter S.R. & Kitchell J.F. (1999). Trophic cascades revealed in diverse ecosystems. *Trends in ecology & evolution*, 14, 483-488.
- Paetzold A., Bernet J.F. & Tockner K. (2006). Consumer-specific responses to riverine subsidy pulses in a riparian arthropod assemblage. *Freshwater Biology*, 51, 1103-1115.
- Paetzold A., Lee M. & Post D. (2008). Marine resource flows to terrestrial arthropod predators on a temperate island: the role of subsidies between systems of similar productivity. *Oecologia*, 157, 653-659.
- Paetzold A., Schubert C.J. & Tockner K. (2005). Aquatic terrestrial linkages along a braided-river: riparian arthropods feeding on aquatic insects. *Ecosystems*, 8, 748-759.
- Paine R. (1992). Food-web analysis through field measurement of per capita interaction strength. *Nature*, 355, 73-75.

- Paine R.T. (1980). Food webs: linkage, interaction strength and community infrastructure. *Journal of Animal Ecology*, 49, 667-685.
- Palmen E. (1944). Die anemohydrochore Ausbreitung der Insekten als zoogeographischer Faktor mit besonderer Berücksichtigung der baltischen Einwanderungsrichtung als Ankunfts- und Ausbreitungsweg der Fennoskandischen Käferfauna. *Annales Zoologici Societatis Zoologicae Botanicae Fennicae Vanamo*, 10.
- Peltzer D.A., Wardle D.A., Allison V.J., Baisden W.T., Bardgett R.D., Chadwick O.A., Condon L.M., Parfitt R.L., Porder S. & Richardson S.J. (2010). Understanding ecosystem retrogression. *Ecological Monographs*, 80, 509-529.
- Pereira H.M., Proenca V.M. & Vicente L. (2007). Does species diversity really drive speciation? *Ecography*, 30, 328-330.
- Persson L., Diehl S., Johansson L., Andersson G. & Hamrin S.F. (1992). Trophic interactions in temperate lake ecosystems: a test of food chain theory. *American Naturalist*, 140, 59-84.
- Petchey O.L., McPhearson P.T., Casey T.M. & Morin P.J. (1999). Environmental warming alters food-web structure and ecosystem function. *Nature*, 402, 69-72.
- Phillips D. & Gregg J. (2003). Source partitioning using stable isotopes: coping with too many sources. *Oecologia*, 136, 261-269.
- Pimm S. & Lawton J. (1978). On feeding on more than one trophic level. *Nature*, 275, 542-1086.
- Pimm S.L. & Lawton J.H. (1977). Number of trophic levels in ecological communities. *Nature*, 268, 329-331.
- Pimm S.L. & Lawton J.H. (1980). Are food webs divided into compartments? *The Journal of Animal Ecology*, 879-1777.
- Pimm S.L., Lawton J.H. & Cohen J.E. (1991). Food web patterns and their consequences. *Nature*, 350, 669-674.
- Polis G. (1988). Exploitation competition and the evolution of interference, cannibalism, and intraguild predation in age/size-structured populations. In: *Size-structured populations*. Springer, pp. 185-202.
- Polis G.A. (1991). Complex Trophic Interactions in Deserts: An Empirical Critique of Food-Web Theory. *The American Naturalist*, 138, 123-155.
- Polis G.A. (1999). Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. *Oikos*, 86, 3-15.
- Polis G.A. & Holt R.D. (1992). Intraguild predation: the dynamics of complex trophic interactions. *Trends in ecology & evolution*, 7, 151-154.
- Polis G.A. & Hurd S.D. (1995). Extraordinarily high spider densities on islands: flow of energy from the marine to terrestrial food webs and the absence of predation. *Proceedings of the National Academy of Sciences*, 92, 4382-4386.
- Polis G.A. & Hurd S.D. (1996). Allochthonous input across habitats, subsidized consumers, and apparent trophic cascades: examples from the ocean-land interface. In: *Food Webs*. Springer, pp. 275-285.
- Polis G.A., Myers C.A. & Holt R.D. (1989). The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics*, 20, 297-330.
- Polis G.A., Power M.E. & Huxel G.R. (2004). *Food webs at the landscape level*. University of Chicago Press, Chicago.
- Polis G.A., Sears A.L., Huxel G.R., Strong D.R. & Maron J. (2000). When is a trophic cascade a trophic cascade? *Trends in ecology & evolution*, 15, 473-475.
- Polis G.A. & Strong D.R. (1996). Food web complexity and community dynamics. *American naturalist*, 147, 813-846.
- Post D., Layman C., Arrington D.A., Takimoto G., Quattrochi J. & Montoya C. (2007). Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia*, 152, 179-189.
- Post D., Pace M. & Hairston N. (2000a). Ecosystem size determines food-chain length in lakes. *Nature*, 405, 1047-1049.
- Post D. & Takimoto G. (2007). Proximate structural mechanisms for variation in food-chain length. *Oikos*, 116, 775-782.

- Post D.M. (2002a). The long and short of food-chain length. *Trends in Ecology & Evolution*, 17, 269-546.
- Post D.M. (2002b). Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology*, 83, 703-718.
- Post D.M. (2007). Testing the productive-space hypothesis: rational and power. *Oecologia*, 153, 973-984.
- Post D.M., Pace M.L. & Hairston N.G. (2000b). Ecosystem size determines food-chain length in lakes. *Nature*, 405, 1047-1049.
- Preston F. (1960). Time and space and the variation of species. *Ecology*, 41, 611-627.
- Raffaelli D. & Hall S.J. (1992). Compartments and predation in an estuarine food web. *Journal of Animal Ecology*, 61, 551-560.
- Raikow D.F., Walters D.M., Fritz K.M. & Mills M.A. (2011). The distance that contaminated aquatic subsidies extend into lake riparian zones. *Ecological Applications*, 21, 983-990.
- Ranta E. & As S. (1982). Non-random colonization of habitat islands by carabid beetles. *Annales Zoologici Fennici*, 19, 175-181.
- RCore (2014). R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing; 2012. *Open access available at: <http://cran.r-project.org>.*
- Rezende E.L., Albert E.M., Fortuna M.A. & Bascompte J. (2009). Compartments in a marine food web associated with phylogeny, body mass, and habitat structure. *Ecology Letters*, 12, 779-788.
- Richardson J.S., Zhang Y. & Marczak L.B. (2010). Resource subsidies across the land–freshwater interface and responses in recipient communities. *River Research and Applications*, 26, 55-66.
- Rickers S., Langel R. & Scheu S. (2006). Stable isotope analyses document intraguild predation in wolf spiders (Araneae: Lycosidae) and underline beneficial effects of alternative prey and microhabitat structure on intraguild prey survival. *Oikos*, 114, 471-478.
- Ricklefs R.E. & Lovette I.J. (1999). The roles of island area per se and habitat diversity in the species-area relationships of four Lesser Antillean faunal groups. *Journal of Animal Ecology*, 68, 1142-1160.
- Ries L. & Sisk T.D. (2010). What is an edge species? The implications of sensitivity to habitat edges. *Oikos*, 119, 1636-1642.
- Roberts M.J. (1987). *The Spiders of Great Britain and Ireland. Linyphiidae and Checklist.-Vol. II.* Harley Books, Chelchester.
- Roberts M.J. (2001). *Collins field guide Spiders of Britain and Northern Europe.* Harper Collins Publishers.
- Rooney N., McCann K., Gellner G. & Moore J.C. (2006). Structural asymmetry and the stability of diverse food webs. *Nature*, 442, 265-269.
- Rose M.D. & Polis G.A. (2000). On the insularity of islands. *Ecography*, 23, 693-701.
- Rubenstein D.R. & Hobson K.A. (2004). From birds to butterflies: animal movement patterns and stable isotopes. *Trends in Ecology & Evolution*, 19, 256-263.
- Samu F. & Szinetár C. (2002). On the nature of agrobiont spiders. *Journal of Arachnology*, 30, 389-402.
- Sanchez-Pinero F. & Polis G.A. (2000). Bottom-up dynamics of allochthonous input: direct and indirect effects of seabirds on islands. *Ecology*, 81, 3117-3132.
- Sanzone D.M., Meyer J.L., Marti E., Gardiner E.P., Tank J.L. & Grimm N.B. (2003). Carbon and nitrogen transfer from a desert stream to riparian predators. *Oecologia*, 134, 238-250.
- Schallhart N., Wallinger C., Juen A. & Traugott M. (2009). Dispersal abilities of adult click beetles in arable land revealed by analysis of carbon stable isotopes. *Agricultural and Forest Entomology*, 11, 333-339.
- Schmidt M.H., Thies C., Nentwig W. & Tschamtk T. (2008). Contrasting responses of arable spiders to the landscape matrix at different spatial scales. *Journal of Biogeography*, 35, 157-166.
- Schmitz O.J., Hambäck P.A. & Beckerman A.P. (2000). Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *The American Naturalist*, 155, 141-153.
- Schoener T.W. (1989). Food webs from the small to the large: The Robert H. MacArthur Award Lecture. *Ecology*, 70, 1559-1589.

- Schoener T.W. (2009). The MacArthur-Wilson Equilibrium Model - A chronicle of what it said and how it was tested. In: *The theory of island biogeography revisited* (eds. Losos JB & Ricklefs RE). Princeton University Press New Jersey, pp. 52 - 87.
- Schoener T.W. & Toft C.A. (1983). Spider populations: extraordinarily high densities on islands without top predators. *Science(Washington)*, 219, 1353-1355.
- Schoenly K. & Cohen J.E. (1991). Temporal variation in food web structure: 16 empirical cases. *Ecological Monographs*, 61, 267-565.
- Semmens B. & Moore J. (2008). MixSIR: A Bayesian stable isotope mixing model. Version 1.04. *EcologyBox, Mathematical Biology Program, Northwest Fisheries Science Center, Seattle*.
- Shea K., Roxburgh S.H. & Rauschert E.S.J. (2004). Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. *Ecology Letters*, 7, 491-508.
- Sheppard S.K. & Harwood J.D. (2005). Advances in molecular ecology: tracking trophic links through predator-prey food-webs. *Functional Ecology*, 19, 751-762.
- Shmida A. & Wilson M.V. (1985). Biological determinants of species diversity. *Journal of Biogeography*, 12, 1-20.
- Shurin J.B., Borer E.T., Seabloom E.W., Anderson K., Blanchette C.A., Broitman B., Cooper S.D. & Halpern B.S. (2002). A cross-ecosystem comparison of the strength of trophic cascades. *Ecology Letters*, 5, 785-791.
- Shurin J.B., Gruner D.S. & Hillebrand H. (2006). All wet or dried up? Real differences between aquatic and terrestrial food webs. *Proceedings of the Royal Society B: Biological Sciences*, 273, 1-9.
- Simberloff D. & Abele L. (1976). Island biogeography theory and conservation practice. *Science (New York, N.Y.)*, 191, 285-291.
- Simberloff D.S. & Wilson E.O. (1969). Experimental zoogeography of islands: the colonization of empty islands. *Ecology*, 50, 278-296.
- Simberloff D.S. & Wilson E.O. (1970). Experimental zoogeography of islands. A two-year record of colonization. *Ecology*, 51, 934-937.
- Snyder W.E. & Wise D.H. (1999). Predator Interference and the Establishment of Generalist Predator Populations for Biocontrol. *Biological Control*, 15, 283-292.
- Solow A.R. & Beet A.R. (1998). On lumping species in food webs. *Ecology*, 79, 2013-2018.
- Sotiropoulos M., Tonn W. & Wassenaar L. (2004). Effects of lipid extraction on stable carbon and nitrogen isotope analyses of fish tissues: potential consequences for food web studies. *Ecology of Freshwater Fish*, 13, 155-160.
- Spence K. & Rosenheim J. (2005). Isotopic enrichment in herbivorous insects: a comparative field-based study of variation. *Oecologia*, 146, 89-186.
- Spencer M. & Warren P.H. (1996). The Effects of Habitat Size and Productivity on Food Web Structure in Small Aquatic Microcosms. *Oikos*, 75, 419-430.
- Spiller D.A. & Schoener T.W. (1988). An experimental study of the effect of lizards on web-spider communities. *Ecological Monographs*, 58, 58-77.
- Stapp P. & Polis G.A. (2003). Influence of pulsed resources and marine subsidies on insular rodent populations. *Oikos*, 102, 111-123.
- Stapp P., Polis G.A. & Pinerio F.S. (1999). Stable isotopes reveal strong marine and El Nino effects on island food webs. *Nature*, 401, 467-469.
- StatSoft (2007). STATISTICA (data analysis software system), version 8.0 [www.statsoft.com](http://www.statsoft.com).
- Sterner R.W., Bajpai A. & Adams T. (1997). The enigma of food chain length: absence of theoretical evidence for dynamic constraints. *Ecology*, 78, 2258-2262.
- Sterner R.W. & Elser J.J. (2002). *Ecological stoichiometry: the biology of elements from molecules to the biosphere*. Princeton University Press.
- Stone L. & Roberts A. (1990). The checkerboard score and species distributions. *Oecologia*, 85, 74-79.
- Stouffer D.B. & Bascompte J. (2011). Compartmentalization increases food-web persistence. *Proceedings of the National Academy of Sciences*, 108, 3648-3652.
- Strong D.R. & Rey J.R. (1982). Testing for MacArthur-Wilson equilibrium with the arthropods of the miniature Spartina archipelago at Oyster Bay, Florida. *American Zoologist*, 22, 355-360.
- Sugihara G., Schoenly K. & Trombla A. (1989). Scale invariance in food web properties. *Science(Washington)*, 245, 48-52.

- Sunderland K., Lovei G. & Fenlon J. (1995). Diets and Reproductive Phenologies of the Introduced Ground Beetles *Harpalus-Affinis* and *Clivina-Australasiae* (Coleoptera, Carabidae) in New-Zealand. *Australian Journal of Zoology*, 43, 39-50.
- Svanbäck R. & Bolnick D.I. (2007). Intraspecific competition drives increased resource use diversity within a natural population. *Proceedings of the Royal Society B: Biological Sciences*, 274, 839-844.
- Sweeting C., Polunin N. & Jennings S. (2006). Effects of chemical lipid extraction and arithmetic lipid correction on stable isotope ratios of fish tissues. *Rapid Communications in Mass Spectrometry*, 20, 595-601.
- Takimoto G., Spiller D.A. & Post D.M. (2008). Ecosystem size, but not disturbance, determines food-chain length on islands of the Bahamas. *Ecology*, 89, 3001- 3007.
- Tansley A.G. (1935). The use and abuse of vegetational concepts and terms. *Ecology*, 16, 284-307.
- Taylor R.M. & Pfannenstiel R.S. (2008). Nectar Feeding by Wandering Spiders on Cotton Plants. *Environmental Entomology*, 37, 996-1002.
- Telfer G. & Butterfield J.E.L. (2004). The control of reproductive diapause in *Nebria salina* (Coleoptera: Carabidae). *Ecological Entomology*, 29, 482-487.
- Ter Braak C. (1988). *CANOCO-a FORTRAN Programme for Canonical Community Ordination by [partial][detrended][canonical] Correspondence Analysis, Principal Components Analysis and Redundancy Analysis (version 2.1)*. Agricultural Mathematics Group.
- Thébault E. & Fontaine C. (2010). Stability of Ecological Communities and the Architecture of Mutualistic and Trophic Networks. *Science*, 329, 853-856.
- Thiele H.-U. (1969). The control of larval hibernation and of adult aestivation in the Carabid beetles *Nebria brevicollis* F. and *Patrobus atrorufus* stroem. *Oecologia*, 2, 347-361.
- Thiele H.-U. (1977). *Carabid beetles in their environments. A study on habitat selection by adaptation in physiology and behaviour*. Springer-Verlag., Heidelberg.
- Thomas C.D. (1994). Extinction, Colonization, and Metapopulations: Environmental Tracking by Rare Species. *Conservation Biology*, 8, 373-378.
- Thompson R., Hemberg M., Starzomski B. & Shurin J. (2007). Trophic levels and trophic tangles: the prevalence of omnivory in real food webs. *Ecology*, 88, 612-619.
- Thompson R., Hemberg M., Starzomski B.M. & Shurin J. (2009). The ubiquity of omnivory. *Verh. Internat. Verein. Limnol*, 30, 761-764.
- Thompson R. & Townsend C. (2005). Energy availability, spatial heterogeneity and ecosystem size predict food-web structure in streams. *Oikos*, 108, 137-148.
- Thornton I.W.B., Zanna R.A. & Van Balen S. (1993). Colonization of Rakata (Krakatau Is.) by non-migrant land birds from 1883 to 1992 and implications for the value of island equilibrium theory. *Journal of Biogeography*, 20, 441-452.
- Tjørve E. & Tjørve K.M.C. (2011). Subjecting the theory of the small-island effect to Ockham's razor. *Journal of Biogeography*, 38, 1836-1839.
- Toft C.A. & Schoener T.W. (1983). Abundance and diversity of orb spiders on 106 Bahamian islands: biogeography at an intermediate trophic level. *Oikos*, 41, 411-426.
- Triantis K., Vardinoyannis K., Tsolaki E., Botsaris I., Lika K. & Mylonas M. (2006). Re-approaching the small island effect. *Journal of Biogeography*, 33, 914-923.
- Triantis K.A., Mylonas M., Weiser M.D., Lika K. & Vardinoyannis K. (2005). Species richness, environmental heterogeneity and area: a case study based on land snails in Skyros archipelago (Aegean Sea, Greece). *Journal of Biogeography*, 32, 1727-1735.
- Turin H., Blankevoort B., Bosch E.J. & van Noortwijk I. (2000). *De Nederlandse loopkevers : verspreiding en oecologie (Coleoptera: Carabidae)*. Nationaal Natuurhistorisch Museum Naturalis [etc.], Leiden [etc.].
- Ueno Y., Hori M., Noda T. & Mukai H. (2006). Effects of material inputs by the Grey Heron *Ardea cinerea* on forest-floor necrophagous insects and understory plants in the breeding colony. *Ornithological Science*, 5, 199-209.
- Uetz G. (1991). Habitat structure and spider foraging. In: *Habitat structure*. Springer, pp. 325-348.
- Ulrich W. (2004). Species co-occurrences and neutral models: reassessing J. M. Diamond's assembly rules. *Oikos*, 107, 603-609.



- Van Eerden M.R., Drent R.H., Stahl J. & Bakker J.P. (2005). Connecting seas: western Palaearctic continental flyway for water birds in the perspective of changing land use and climate. *Global Change Biology*, 11, 894-908.
- Vander Zanden M.J., Shuter B.J., Lester N. & Rasmussen J.B. (1999). Patterns of food chain length in lakes: a stable isotope study. *The American Naturalist*, 154, 406-416.
- Vanderklift M.A. & Ponsard S. (2003). Sources of variation in consumer-diet  $\delta^{15}\text{N}$  enrichment: a meta-analysis. *Oecologia*, 136, 169-182.
- Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R. & Cushing C.E. (1980). The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, 37, 130-137.
- Wada E., Kadonaga T. & Matsuo S. (1975).  $^{15}\text{N}$  abundance in nitrogen of naturally occurring substances and global assessment of denitrification from isotopic viewpoint. *Geochem. J.*, 9, 139-148.
- Wainright S., Haney J., Kerr C., Golovkin A. & Flint M. (1998). Utilization of nitrogen derived from seabird guano by terrestrial and marine plants at St. Paul, Pribilof Islands, Bering Sea, Alaska. *Marine Biology*, 131, 63-71.
- Walter H.S. (2004). The mismeasure of islands: implications for biogeographical theory and the conservation of nature. *Journal of Biogeography*, 31, 177-197.
- Walters A.W. & Post D.M. (2008). An experimental disturbance alters fish size structure but not food chain length in streams. *Ecology*, 89, 3261-3267.
- Walters D.M., Fritz K.M. & Otter R.R. (2008). The dark side of subsidies: adult stream insects export organic contaminants to riparian predators. *Ecological Applications*, 18, 1835-1841.
- Wardle D.A., Zackrisson O., Hörnberg G. & Gallet C. (1997). The influence of island area on ecosystem properties. *Science*, 277, 1296-1299.
- Weigelt P. & Kreft H. (2013). Quantifying island isolation - insights from global patterns of insular plant species richness. *Ecography*, 36, 417-429.
- Wesner J.S. (2010). Seasonal variation in the trophic structure of a spatial prey subsidy linking aquatic and terrestrial food webs: adult aquatic insects. *Oikos*, 119, 170-178.
- Whittaker R.H. (1972). Evolution and measurement of species diversity. *Taxon*, 21, 213-251.
- Whittaker R.J. (2000). Scale, succession and complexity in island biogeography: are we asking the right questions? *Global Ecology and Biogeography*, 9, 75-85.
- Wiens J.A., Crawford C.S. & Gosz J.R. (1985). Boundary Dynamics: A Conceptual Framework for Studying Landscape Ecosystems. *Oikos*, 45, 421-427.
- Williams C.B. (1964). *Patterns in the balance of nature*. Academic Press, London.
- Williams D.D., Ambrose L.G. & Browning L.N. (1995). Trophic dynamics of two sympatric species of riparian spider (Araneae: Tetragnathidae). *Canadian Journal of Zoology*, 73, 1545-1553.
- Williams R.J. & Martinez N.D. (2004). Limits to Trophic Levels and Omnivory in Complex Food Webs: Theory and Data. *The American Naturalist*, 163, 458-468.
- Wilson E. & Wolkovich E. (2011). Scavenging: how carnivores and carrion structure communities. *Trends in Ecology & Evolution*, 26, 129-135.
- Wise D.H., Moldenhauer D.M. & Halaj J. (2006). Using stable isotopes to reveal shifts in prey consumption by generalist predators. *Ecological Applications*, 16, 865-876.
- Witman J.D., Ellis J.C. & Anderson W.B. (2004). The influence of physical processes, organisms, and permeability on cross-ecosystem fluxes. In: *Food webs at the landscape level*. University of Chicago Press, Chicago, Illinois, USA (eds. Polis GA, Power ME & Huxel GR). University of Chicago Press Chicago and London, pp. 335-358.
- Woodcock P., Edwards D., Newton R., Edwards F., Khen C., Bottrell S. & Hamer K. (2012). Assessing trophic position from nitrogen isotope ratios: effective calibration against spatially varying baselines. *Naturwissenschaften*, 99, 275-283.
- Wootton J.T. (1994). The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematics*, 25, 443-466.
- Wootton J.T. & Emmerson M. (2005). Measurement of Interaction Strength in Nature. *Annual Review of Ecology, Evolution, and Systematics*, 36, 419-444.
- Wootton J.T., Power M.E., Paine R.T. & Pfister C.A. (1996). Effects of productivity, consumers, competitors, and El Niño events on food chain patterns in a rocky intertidal community. *Proceedings of the National Academy of Sciences*, 93, 13855-13858.

- Yang L.H., Bastow J.L., Spence K.O. & Wright A.N. (2008). What can we learn from resource pulses. *Ecology*, 89, 621-634.
- Yodzis P. (1984). Energy flow and the vertical structure of real ecosystems. *Oecologia*, 65, 86-88.
- Young H.S., McCauley D.J., Dunbar R.B. & Dirzo R. (2010). Plants cause ecosystem nutrient depletion via the interruption of bird-derived spatial subsidies. *Proceedings of the National Academy of Sciences*, 107, 2072-2077.
- Young H.S., McCauley D.J., Dunbar R.B., Hutson M.S., Ter-Kuile A.M. & Dirzo R. (2013). The roles of productivity and ecosystem size in determining food chain length in tropical terrestrial ecosystems. *Ecology*, 94, 692-701.
- Zalewski M. (2004). Do smaller islands host younger populations? A case study on metapopulations of three carabid species. *Journal of Biogeography*, 31, 1139-1148.
- Zalewski M., Dudek D., Tiunov A.V., Godeau J.-F., Okuzaki Y., Ikeda H., Sienkiewicz P. & Ulrich W. (2014). High niche overlap in the stable isotope space of ground beetles. *Annales Zoologici Fennici*, 51, in press; [preprint online since 28 Nov. 2013]; <http://www.sekj.org/PDF/anz50-free/Zalewski35764-free.pdf>.
- Zalewski M. & Ulrich W. (2006). Dispersal as a key element of community structure: the case of ground beetles on lake islands. *Diversity and Distributions*, 12, 767-775.
- Zera A.J. & Denno R.F. (1997). Physiology and ecology of dispersal polymorphism in insects. *Annual Review of Entomology*, 42, 207-230.

## Appendix A

**Tab. A1** species/site matrix of the sampling in June 2010 on islands and mainland sites for spiders with abbreviations in CCA - plots, assorted to spider families;

Spider species	Island/mainland site																				Abbreviation in CCA-plot
	B1	B2	K8	B11	B11B	B12	BF	D1	D2	D3	D4	D5	D6	D7	D8	D10	DF	DS	DW		
<b>Agelenidae</b>																					
<i>Histopona torpida</i> (C.L. Koch, 1837)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0		
<i>Textrix denticulata</i> (Olivier, 1789)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0		
<b>Araneidae</b>																					
<i>Larinionides sclopetarius</i> (Clerck, 1757)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0		
<b>Clubionidae</b>																					
<i>Clubiona frisia</i> (Wunderlich & Schuett, 1995)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0		
<i>Clubiona lutescens</i> (Westring, 1851)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4		
<i>Clubiona neglecta</i> (O. P.-Cambridge, 1862)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Clubiona pallidula</i> (Clerck, 1757)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0		
<i>Clubiona phragmitis</i> (C. L. Koch, 1843)	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	0	0	1		
<i>Clubiona</i> sp.	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0		
<b>Gnaphosidae</b>																					
<i>Callilepis nocturna</i> (Linnaeus, 1758)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0		
<i>Drassodes cupreus</i> (Blackwall, 1834)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0		
<i>Drassodes pubescens</i> (Thorell, 1856)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0		
<i>Micaria pulicaria</i> (Sundevall, 1831)	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0		
<i>Micaria silesiaca</i> (L. Koch, 1875)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Zelotes apricorum</i> (L. Koch, 1876)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1		
<i>Trachyzelotes pedestris</i> (C. L. Koch, 1837)	0	16	1	0	0	0	11	0	1	0	2	0	1	2	0	3	3	16	103	Tracpede	
<i>Drassyllus praeficus</i> (L. Koch, 1866)	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1		
<i>Drassyllus pusillus</i> (C. L. Koch, 1833)	1	1	8	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	1	Draspusi	
<i>Zelotes subterraneus</i> (C. L. Koch, 1833)	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0	0		
<b>Hahnidae</b>																					

Spider species	Island/mainland site																		Abbreviation in CCA-plot		
	B1	B2	K8	B11	B11B	B12	BF	D1	D2	D3	D4	D5	D6	D7	D8	D10	DF	DS		DW	
<i>Hahnia nava</i> (Blackwall, 1841)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<u>Liocranidae</u>																					
<i>Apostenus fuscus</i> (Westring, 1851)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
<u>Corinnidae</u>																					
<i>Phrurolithus festivus</i> (C. L. Koch, 1835)	0	5	1	0	0	0	3	0	0	9	3	1	8	3	1	0	0	2	7	Phrufest	
<i>Phrurolithus minimus</i> (C. L. Koch, 1839)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0		
<u>Lycosidae</u>																					
<i>Alopecosa cuneata</i> (Clerck, 1757)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0		
<i>Arctosa cinerea</i> (Fabricius, 1777)	0	0	0	0	0	0	0	0	0	0	1	1	4	16	14	4	0	0	0	Arctcine	
<i>Arctosa leopardus</i> (Sundevall, 1833)	11	13	103	15	20	50	26	0	2	0	33	30	37	9	2	4	20	18	2	Arctleop	
<i>Arctosa perita</i> (Latreille, 1799)	0	0	0	0	0	0	0	0	0	0	8	9	5	7	5	0	0	0	0	Arctperi	
<i>Pardosa agrestis</i> (Westring, 1861)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0		
<i>Pardosa agricola</i> (Thorell, 1856)	0	0	0	0	0	0	1	0	0	0	1	1	2	0	0	0	0	0	0	Pardagri	
<i>Pardosa amentata</i> (Clerck, 1757)	0	0	0	0	0	0	0	0	0	0	0	2	4	6	0	0	38	1	10	Pardamen	
<i>Pardosa fulvipes</i> (Collett, 1876)	0	0	0	1	0	0	0	0	0	0	0	3	1	0	0	1	7	2	0	Pardfulv	
<i>Pardosa lugubris</i> (Walckenaer, 1802)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	5	84	Pardlugu	
<i>Pardosa monticola</i> (Clerck, 1757)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Pardosa palustris</i> (Linnaeus, 1758)	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	Pardpalu	
<i>Pardosa prativaga</i> (L. Koch, 1870)	13	32	49	2	1	3	17	0	1	0	0	13	18	4	0	0	23	15	8	Pardprat	
<i>Pardosa pullata</i> (Clerck, 1757)	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Pardpull	
<i>Pardosa sphagnicola</i> (Dahl, 1908)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0		
<i>Piratula insularis</i> (Emerton, 1885)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0		
<i>Piratula hygrophila</i> (Thorell, 1872)	0	0	4	0	1	1	0	0	0	0	1	0	1	0	1	6	52	1	121	Pirahygr	
<i>Piratula latitans</i> (Blackwall, 1841)	0	0	1	0	0	0	2	0	0	0	0	0	0	1	1	0	0	0	0	Piralati	
<i>Pirata piraticus</i> (Clerck, 1757)	2	0	2	1	2	1	0	0	0	0	0	0	1	0	0	0	1	0	0	Pirapira	
<i>Pirata tenuitarsis</i> (Simon, 1876)	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0		
<i>Trochosa ruricola</i> (De Geer, 1778)	1	41	8	2	0	2	34	0	1	0	37	30	19	13	4	3	49	10	6	Trocruri	

Spider species	Island/mainland site																		Abbreviation in CCA-plot	
	B1	B2	K8	B11	B11B	B12	BF	D1	D2	D3	D4	D5	D6	D7	D8	D10	DF	DS		DW
<i>Trochosa robusta</i> (Simon, 1876)	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	2	0	0	
<i>Trochosa terricola</i> (Thorell, 1856)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	
<i>Xerolycosa miniata</i> (C. L. Koch, 1834)	0	16	0	0	0	0	9	0	0	3	206	98	51	10	123	0	5	40	1	Xeromini
<i>Xerolycosa nemoralis</i> (Westring, 1861)	0	1	0	0	0	0	0	0	0	0	0	12	0	1	12	0	0	0	0	Xeronemo
<u>Linyphiidae</u>																				
<i>Bathyphantes gracilis</i> (Blackwall, 1841)	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Batyphantes setiger</i> (F. O. P.-Cambridge, 1894)	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	
<i>Ceratinella scabrosa</i> (O. P.-Cambridge, 1871)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	
<i>Diplocephalus latifrons</i> (O. P.-Cambridge, 1863)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	
<i>Diplocephalus picinus</i> (Blackwall, 1841)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Diplostyla concolor</i> (Wider, 1834)	0	0	0	0	0	0	0	0	1	2	0	0	0	0	1	1	1	0	2	Diplconc
<i>Erigone arctica</i> (White, 1852)	0	0	0	0	0	0	0	0	2	0	0	0	2	0	1	44	1	0	0	Erigarct
<i>Erigone atra</i> (Blackwall, 1833)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	
<i>Erigone dentipalpis</i> (Wider, 1834)	0	1	0	0	0	0	0	14	72	0	5	2	4	0	2	144	1	4	0	Erigdent
<i>Erigone longipalpis</i> (Sundevall, 1830)	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	27	0	0	0	Eriglong
<i>Prinerigone vagans</i> (Audouin, 1826)	0	0	0	0	0	1	0	2	2	0	0	0	0	0	0	5	0	0	0	Prinvaga
<i>Gonatium rubens</i> (Blackwall, 1833)	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	
<i>Gongylidium rufipes</i> (Linnaeus, 1758)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Halorates reprobus</i> (O. P.-Cambridge, 1879)	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	
<i>Tenuiphantes tenuis</i> (Blackwall, 1852)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Tenuiphantes flavipes</i> (Blackwall, 1854)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
<i>Tenuiphantes zimmermanni</i> (Bertkau, 1890)	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	
<i>Maso sundevalli</i> (Westring, 1851)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	Meiorure
<i>Agyneta rurestris</i> (C. L. Koch, 1836)	0	0	0	0	0	0	0	0	3	0	0	0	0	0	6	39	0	0	0	
<i>Collinsia inerrans</i> (O. P.-Cambridge, 1885)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	
<i>Neriene clathrata</i> (Sundevall, 1830)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Oedothorax apicatus</i> (Blackwall, 1850)	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	1	0	0	0	Oedoapi

Spider species	Island/mainland site																		Abbreviation in CCA-plot	
	B1	B2	K8	B11	B11B	B12	BF	D1	D2	D3	D4	D5	D6	D7	D8	D10	DF	DS		DW
<i>Oedothorax fuscus</i> (Blackwall, 1834)	0	0	12	3	0	1	0	0	9	0	0	0	0	0	0	3	1	0	0	Oedofusc
<i>Oedothorax retusus</i> (Westring, 1851)	17	6	24	1	1	23	0	7	3	0	0	0	0	0	0	0	32	1	0	Oedoretu
<i>Pelecopsis parallela</i> (Wider, 1834)	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	
<i>Silometopus elegans</i> (O. P.-Cambridge, 1872)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	
<i>Syedra gracilis</i> (Menge, 1869)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	
<i>Troxochrus scabriculus</i> (Westring, 1851)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Walckenaeria furcillata</i> (Menge, 1869)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Walckenaeria vigilax</i> (Blackwall, 1853)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
<u>Philodromidae</u>																				
<i>Philodromus aureolus</i> (Clerck, 1757)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	
<u>Pisauridae</u>																				
<i>Pisaura mirabilis</i> (Clerck, 1757)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	Pisamira
<u>Salticidae</u>																				
<i>Euophrys frontalis</i> (Walckenaer, 1802)	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Phlegra fasciata</i> (Hahn, 1826)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	
<i>Salticus scenicus</i> (Clerck, 1757)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Synageles venator</i> (Lucas, 1836)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	
<u>Theriidae</u>																				
<i>Enoplognatha latimana</i> (Hippa & Oksala, 1982)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	
<i>Euryopsis flavomaculata</i> (C. L. Koch, 1836)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	2	
<u>Thomisidae</u>																				
<i>Ozyptila praticola</i> (C. L. Koch, 1837)	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	11	0	15	
<i>Ozyptila trux</i> (Blackwall, 1846)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	
<i>Xysticus kochi</i> (Thorell, 1872)	0	0	0	0	0	0	0	0	0	0	1	3	0	0	0	0	0	0	0	
<u>Tetragnathidae</u>																				
<i>Pachygnatha clercki</i> (Sundevall, 1823)	1	3	12	6	0	3	3	4	4	0	2	0	0	1	0	2	1	2	7	
<i>Pachygnatha degeeri</i> (Sundevall, 1830)	0	8	0	0	0	0	13	0	0	0	1	0	1	0	0	1	3	5	44	

Spider species	Island/mainland site																		Abbreviation in CCA-plot
	B1	B2	K8	B11	B11B	B12	BF	D1	D2	D3	D4	D5	D6	D7	D8	D10	DF	DS	
<i>Pachygnatha listeri</i> (Sundevall, 1830)	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	1
<i>Tetragnatha extensa</i> (Linnaeus, 1758)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Tetragnatha</i> sp.	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0

**Tab. A2** species/site matrix of the sampling in June 2010 on islands and mainland sites for ground beetles with abbreviations in CCA - plots, assorted to spider families;

Ground beetle species	Island/mainland site																		Abbreviation in CCA-plot	
	K2	K8	K11a	K11b	K12	KF	D1	D2	D3	D4	D5	D52	D6	D7	D8	D10	DF	DS		DW
<i>Acupalpus brunnipes</i> (Sturm, 1825)	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	
<i>Acupalpus flavicollis</i> (Sturm, 1825)	0	0	0	0	0	3	0	0	0	1	0	0	0	4	0	0	0	1	0	Acupflav
<i>Acupalpus meridianus</i> (Linné, 1761)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	Acupmeri
<i>Acupalpus parvulus</i> (Sturm, 1825)	0	6	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	Acupparv
<i>Agonum duftschmidi</i> (Schmidt, 1994)	1	4	3	1	13	0	0	0	0	0	0	0	2	0	0	0	0	4	14	Agonduft
<i>Agonum marginatum</i> (Linné, 1758)	0	0	2	0	2	0	2	17	0	0	0	0	0	0	1	5	0	0	0	Agonmarg
<i>Agonum micans</i> (Nicolai, 1822)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	
<i>Agonum muelleri</i> (Herbst, 1784)	0	0	0	0	0	0	0	0	0	0	0	1	3	1	0	0	0	0	0	Agonmuel
<i>Agonum munsteri</i> (Hellén 1935)	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Agonum scitulum</i> (Dejean, 1828)	0	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Agonscit
<i>Agonum viduum</i> (Panzer, 1796)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	4	0	Agonvidu
<i>Agonum viridicupreum</i> (Goeze, 1777)	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Amara aenea</i> (De Geer, 1774)	2	0	0	0	0	2	0	0	7	114	125	71	61	31	107	9	0	4	0	Amaraen
<i>Amara communis</i> (Panzer, 1797)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	11	Amarcomm

Ground beetle species	Island/mainland site																		Abbreviation in CCA-plot	
	K2	K8	K11a	K11b	K12	KF	D1	D2	D3	D4	D5	D52	D6	D7	D8	D10	DF	DS		DW
<i>Amara bifrons</i> (Gyllenhal, 1810)	0	0	0	0	0	0	0	2	25	3	1	4	1	1	1	1	0	0	0	Amarbifr
<i>Amara fulva</i> (O.F. Müller, 1776)	0	0	0	0	0	0	0	0	0	0	0	0	0	6	1	5	0	0	0	Amarfulv
<i>Amara majuscula</i> (Chaudoir, 1850)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	
<i>Amara nitida</i> (Sturm, 1825)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	
<i>Anchomenus dorsalis</i> (Pontoppidan, 1763)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	Anchdors
<i>Anisodactylus binotatus</i> (Fabricius, 1787)	0	4	1	0	1	2	0	14	23	3	0	0	0	1	4	11	10	4	3	Anisduct
<i>Badister bullatus</i> (Schränk, 1798)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	
<i>Badister meridionalis</i> (Puel, 1925)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	
<i>Bembidion articulatum</i> (Panzer, 1796)	0	1	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Bembidion biguttatum</i> (Fabricius 1779)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	
<i>Bembidion dentellum</i> (Thunberg, 1787)	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	
<i>Benmbidion femoratum</i> (Sturm, 1825)	0	0	0	0	0	0	16	1	4	0	0	0	1	2	1	83	0	0	0	Bembfemo
<i>Bembidion illigeri</i> (Netolitzky, 1914)	0	0	0	0	0	0	0	0	1	1	0	2	0	0	0	0	0	0	0	
<i>Bembidion lampros</i> (Herbst, 1784)	6	0	0	0	0	3	0	0	16	1	2	0	0	0	4	1	1	0	0	Bemblamp
<i>Bembidion lunulatum</i> (Geoffroy, 1785)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	
<i>Bembidion punctulatum</i> (Drapiez, 1820)	0	0	0	0	0	0	2	0	0	1	0	0	0	0	1	0	0	1	0	Bempunc
<i>Bembidion quadrimaculatum</i> (Linné, 1761)	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	20	0	0	0	Bembquad
<i>Bembidion semipunctatum</i> (Donovan, 1806)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	
<i>Bembidion tetracolum</i> (Say, 1823)	0	0	0	0	0	0	3	1	0	0	0	0	1	0	1	14	22	0	7	Bembtetr
<i>Bembidion varium</i> (Olivier, 1795)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Calathus melanocephalus</i> (Linné, 1758)	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	
<i>Carabus cancellatus</i> (Illiger, 1798)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	
<i>Carabus nemoralis</i> (O.F. Müller, 1764)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	
<i>Chlaenius nigricornis</i> (Fabricius, 1787)	0	2	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Chlaenigr
<i>Chlaenius vestitus</i> (Paykull, 1790)	2	0	0	0	0	0	3	6	10	2	0	0	4	11	3	4	0	4	8	Chlaevest
<i>Cicindela hybrida</i> (Linné, 1758)	0	0	0	0	0	0	0	0	0	0	1	1	9	37	5	0	0	3	0	Cichybr
<i>Clivina collaris</i> (Herbst, 1784)	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	

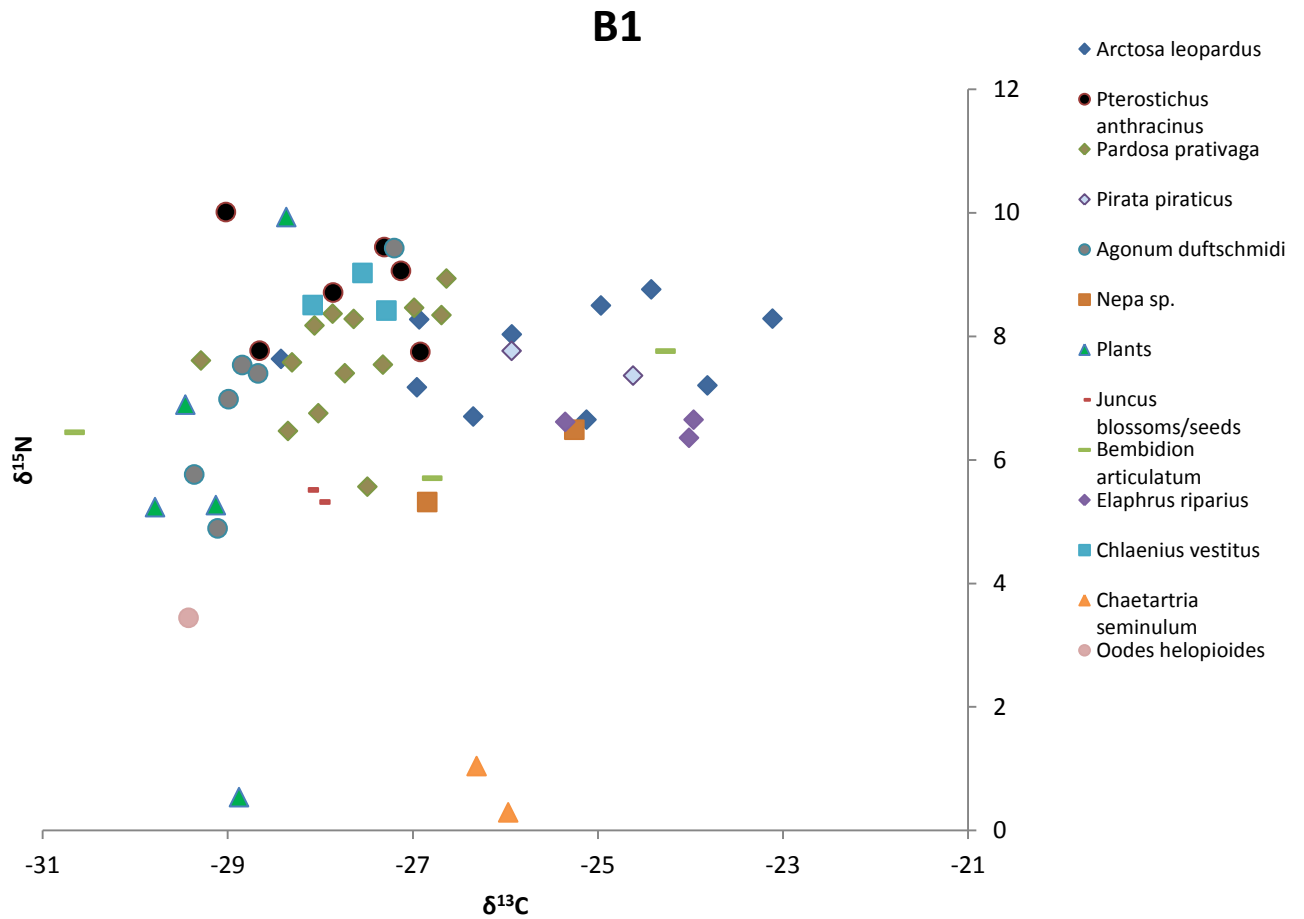


Ground beetle species	Island/mainland site																		Abbreviation in CCA-plot	
	K2	K8	K11a	K11b	K12	KF	D1	D2	D3	D4	D5	D52	D6	D7	D8	D10	DF	DS		DW
<i>Clivina fossor</i> (Linné 1758)	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	2	4	0	0	Clivfoss
<i>Dyschirius thoracicus</i> (P.Rossi, 1790)	0	0	0	0	0	0	5	0	3	1	7	0	3	10	0	1	0	5	1	Dyscthor
<i>Elaphrus cupreus</i> (Duftschmid, 1812)	0	0	1	0	2	0	0	1	0	0	0	0	0	0	0	0	2	0	1	Elapcupr
<i>Elaphrus riparius</i> (Linné 1758)	0	0	0	1	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0	Elapripa
<i>Harpalus affinis</i> (Schrank, 1781)	5	0	0	0	0	2	1	0	20	15	6	9	1	22	6	59	0	0	0	Harpaffi
<i>Harpalus flavicornis</i> (Dejean, 1829)	0	0	0	0	0	0	0	0	0	0	2	2	1	0	0	0	0	0	0	Harpflav
<i>Harpalus rufipalpis</i> (Sturm, 1818)	2	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Harpalus froelichii</i> (Sturm, 1818)	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	
<i>Harpalus luteicornis</i> (Duftschmid 1812)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	
<i>Harpalus marginellus</i> (Gyllenhal, 1827)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	
<i>Harpalus serripes</i> (Quensel in Schönherr, 1806)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	
<i>Lionychnus quadrillum</i> (Duftschmid, 1812)	0	0	0	0	0	0	0	0	10	0	0	0	0	0	2	1	0	0	0	Lionyquad
<i>Loricera pilicornis</i> (Fabricius, 1775)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	
<i>Microlestes minutulus</i> (Goeze, 1775)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Nebria brevicollis</i> (Fabricius, 1792)	0	0	0	0	3	1	0	1	0	3	0	3	2	0	0	6	16	0	0	Nebrbrev
<i>Nebria livida</i> (Linné, 1758)	0	0	0	0	0	0	2	0	0	0	0	0	0	0	5	0	0	0	0	Nebrlivi
<i>Nebria salina</i> (Fairmaire & Laboulb, 1854)	0	0	0	0	0	0	1	1	0	8	7	4	7	5	2	12	0	0	0	Nebrisali
<i>Notiophilus aquaticus</i> (Linné, 1758)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	
<i>Notiophilus palustris</i> (Duftschmid, 1812)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
<i>Notiophilus substriatus</i> (Waterhouse, 1833)	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	
<i>Omophron limbatum</i> (Fabricius, 1776)	0	5	0	0	2	0	0	0	7	0	0	0	24	21	0	0	0	22	0	Omoplimb
<i>Oodes helopiodes</i> (Fabricius, 1792)	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	3	Oodeheli
<i>Ophonus rupicola</i> (Sturm, 1818)	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	
<i>Oxypselaphus obscurus</i> (Herbst, 1784)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	2	2	
<i>Panagaeus cruxmajor</i> (Linné, 1758)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Paradromius linearis</i> (Olivier, 1795)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	
<i>Paranchus albipes</i> (Fabricius, 1796)	0	0	2	0	3	0	1	13	0	0	0	0	1	1	0	1	0	0	2	Paraalbi

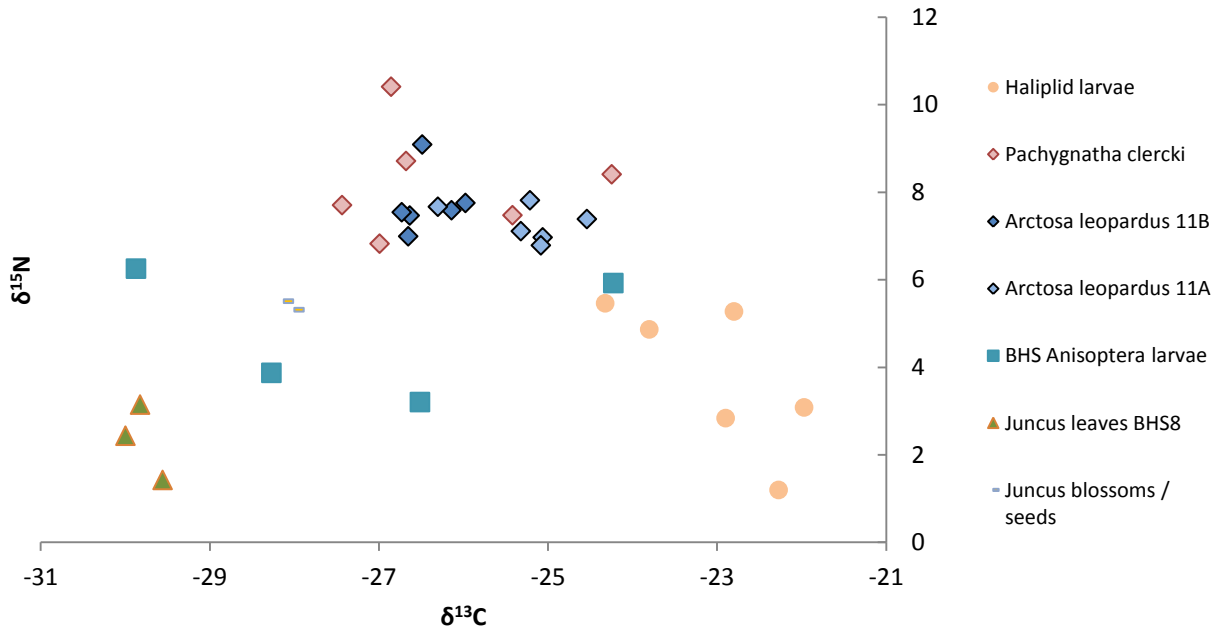
Ground beetle species	Island/mainland site																		Abbreviation in CCA-plot	
	K2	K8	K11a	K11b	K12	KF	D1	D2	D3	D4	D5	D52	D6	D7	D8	D10	DF	DS		DW
<b>Elaphropus parvulus (Fischer v.W., 1828)</b>	0	0	0	0	0	0	0	0	18	8	2	0	3	5	4	21	0	4	0	Paramicr
<b>Poecilus versicolor (Sturm, 1824)</b>	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	2	0	3	9	Poecvers
<b>Pterostichus anthracinus (Illiger, 1798)</b>	0	17	1	0	5	0	0	0	0	0	0	0	0	0	0	0	9	0	8	Pteranth
<b>Pterostichus gracilis (Dejean, 1828)</b>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<b>Pterostichus madidus (Fabricius, 1775)</b>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
<b>Pterostichus melanarius (Illiger, 1798)</b>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	6	0	2	Ptermela
<b>Pterostichus minor (Gyllenhal, 1827)</b>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	
<b>Pterostichus nigrita (Paykull, 1790)</b>	0	3	1	0	14	1	0	0	0	0	0	0	0	0	0	0	29	1	10	Pternigr
<b>Pterostichus strenuus (Panzer, 1796)</b>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	1	1	Pterstre
<b>Pterostichus unctulatus (Duftschmid 1812)</b>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<b>Pterostichus vernalis (Panzer, 1796)</b>	0	0	0	0	1	0	1	0	0	0	0	3	0	0	0	0	3	0	0	Ptervern
<b>Stenolophus mixtus (Herbst, 1784)</b>	0	6	0	0	4	1	0	2	1	0	0	1	0	0	0	0	0	0	0	Stenmixt
<b>Stenolophus teutonius (Schränk, 1781)</b>	0	21	0	0	30	2	0	26	0	12	4	23	19	3	1	23	4	0	0	Stenteut
<b>Stomis pumicatus (Panzer, 1796)</b>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	2	0	Stompumi
<b>Syntomus foveatus (Geoffroy, 1785)</b>	0	0	0	0	0	0	0	0	4	1	0	0	0	0	1	0	0	5	0	Syntfove

## Appendix B

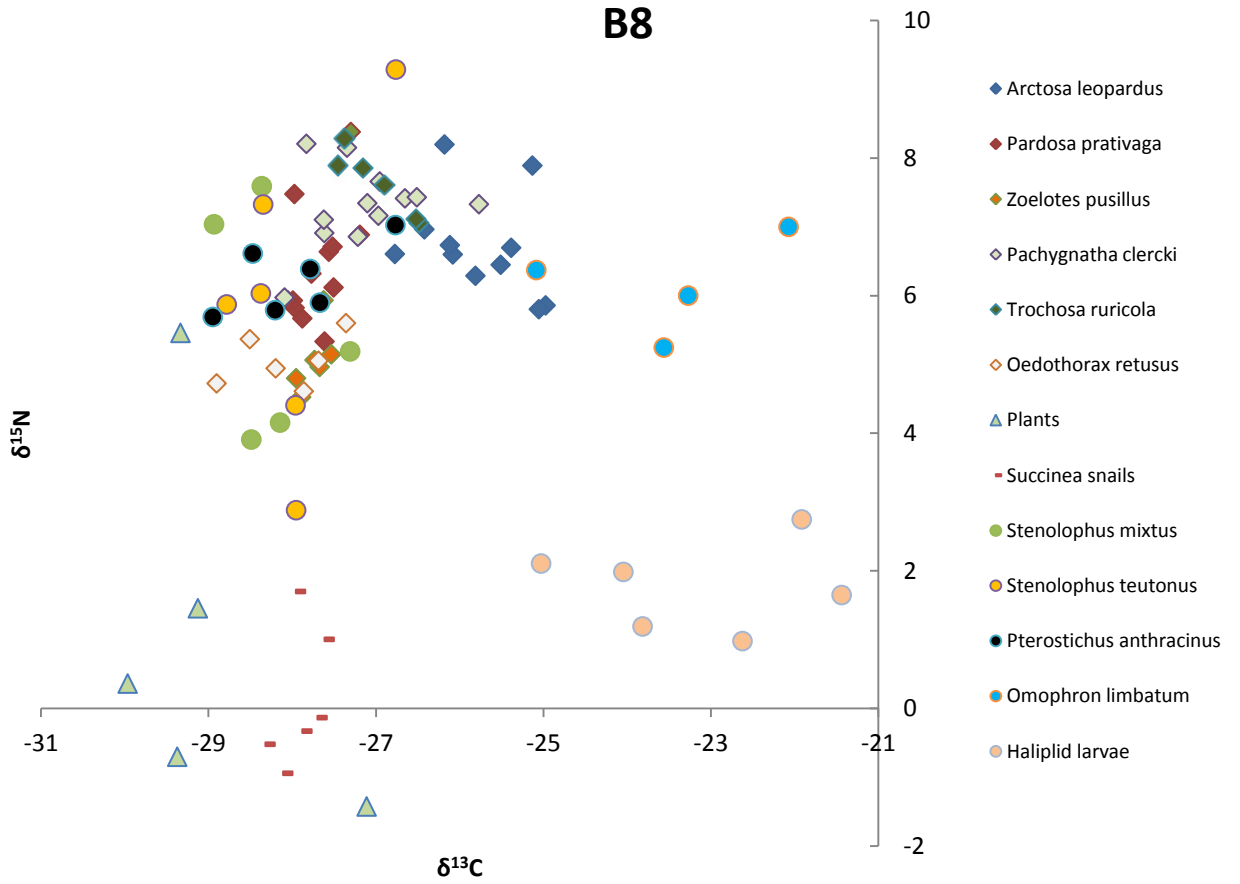
This Appendix contains bi-plots of  $\delta^{13}\text{C}$  to  $\delta^{15}\text{N}$  of each island. Legends are given in the figures. Figure titles indicate island number. Symbols for beetles are always circles, symbols for spiders are always diamonds, symbols for plants are always triangles.



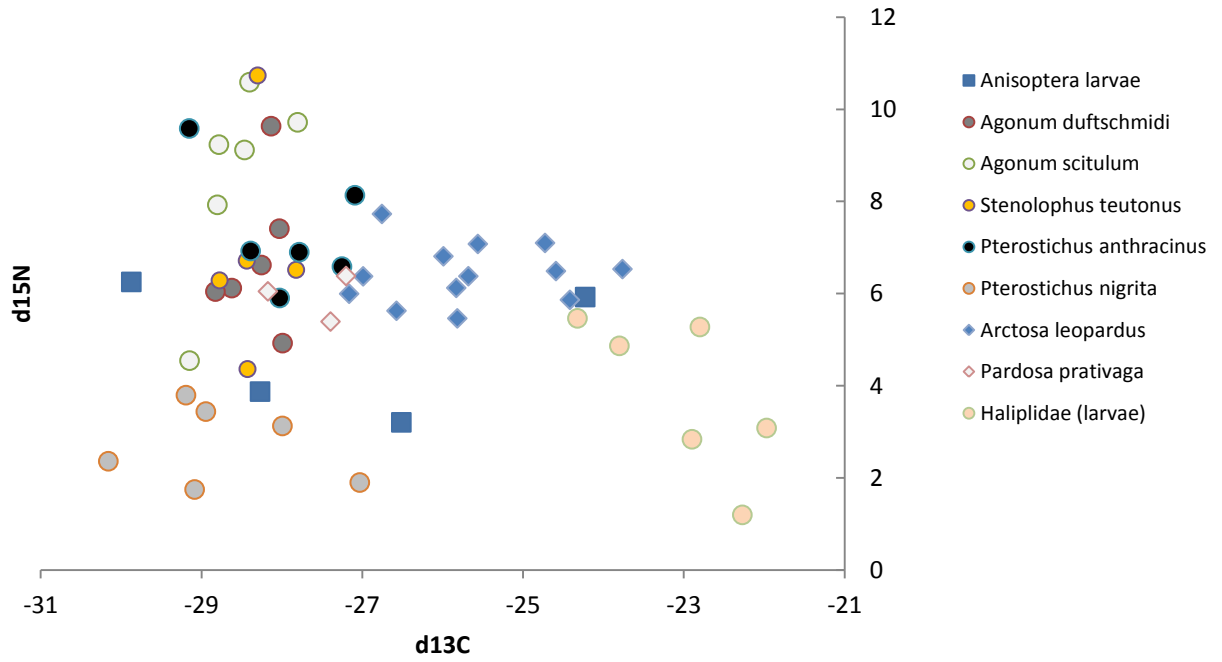
### B11 A&B



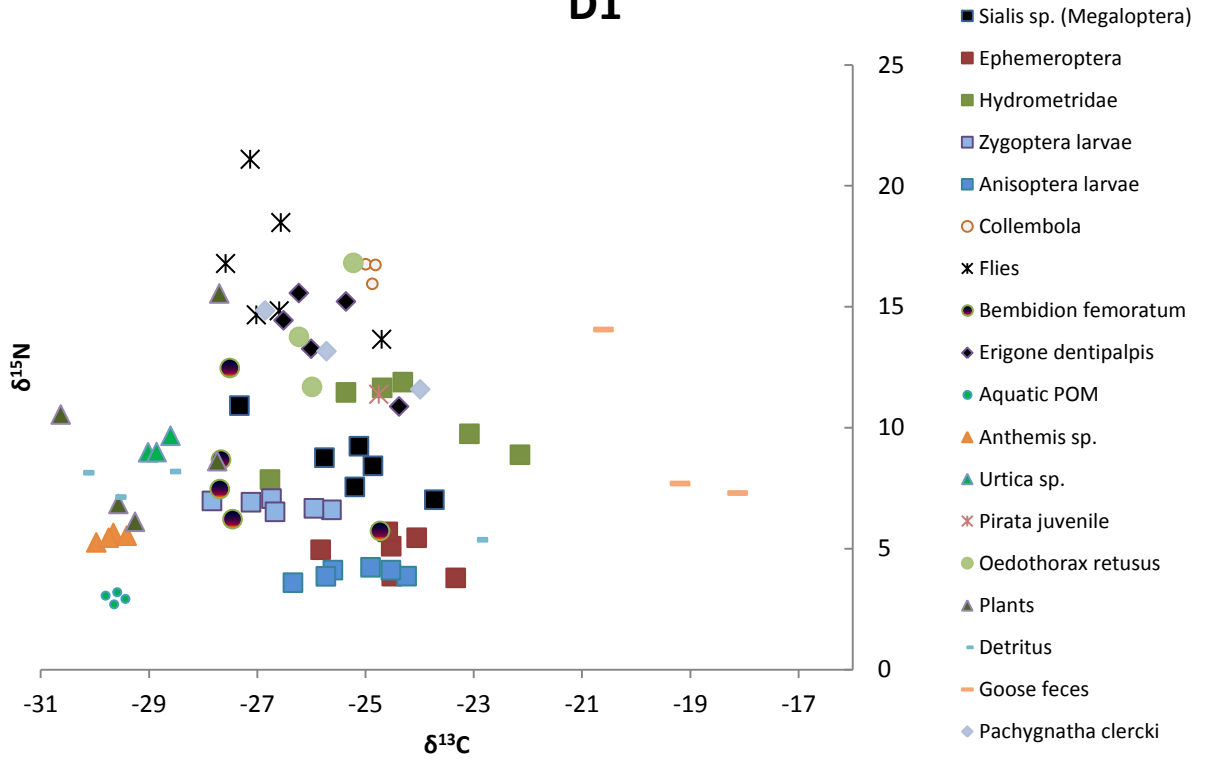
### B8



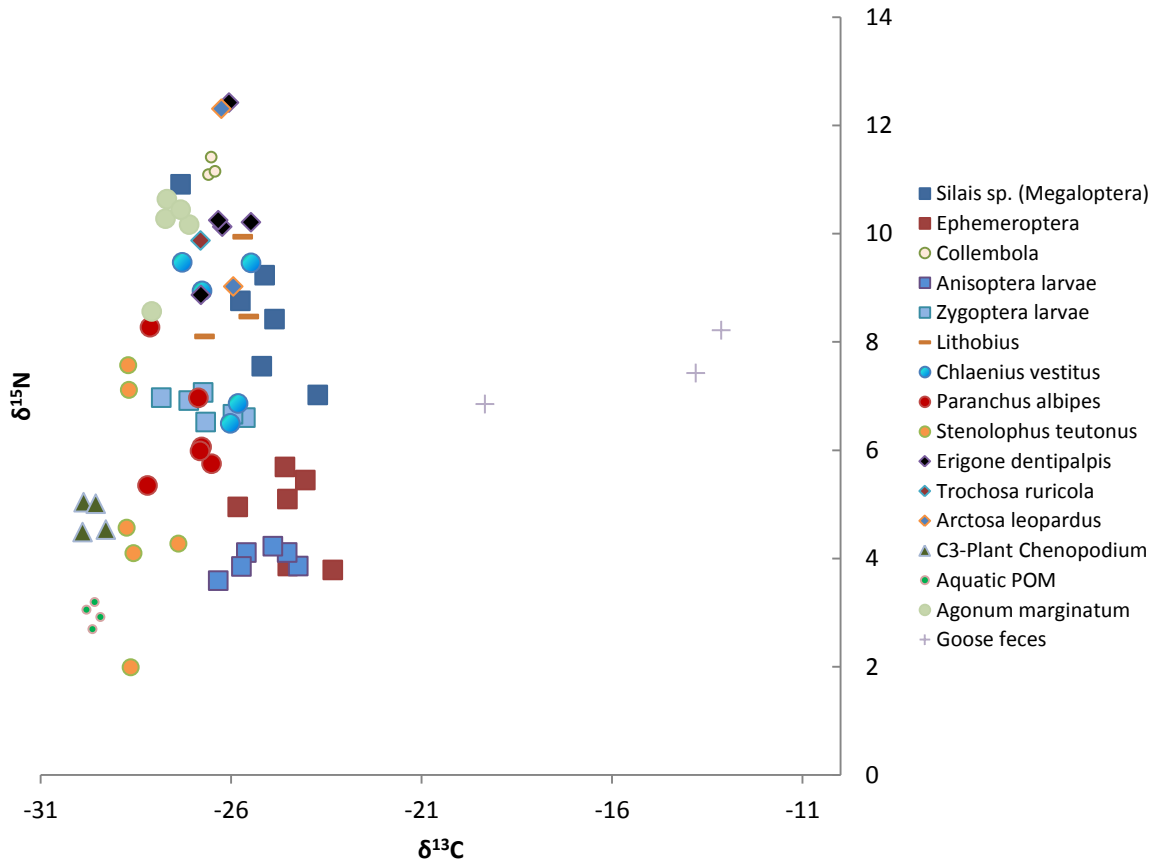
## B12



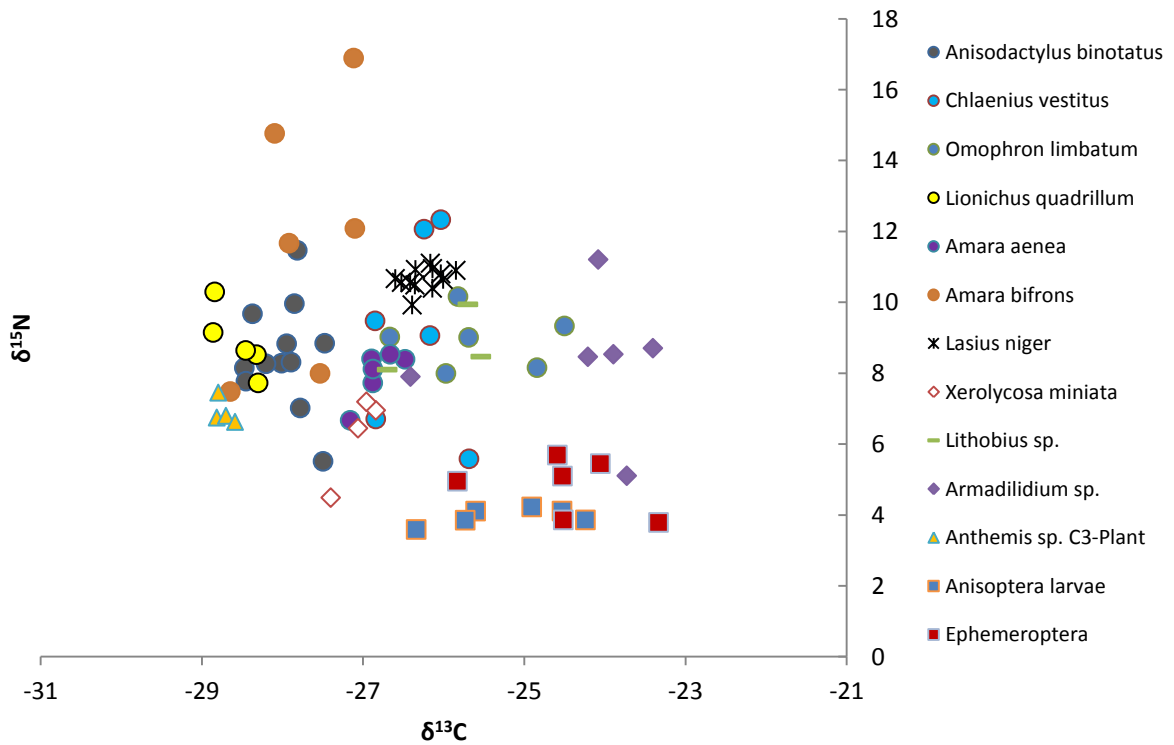
## D1



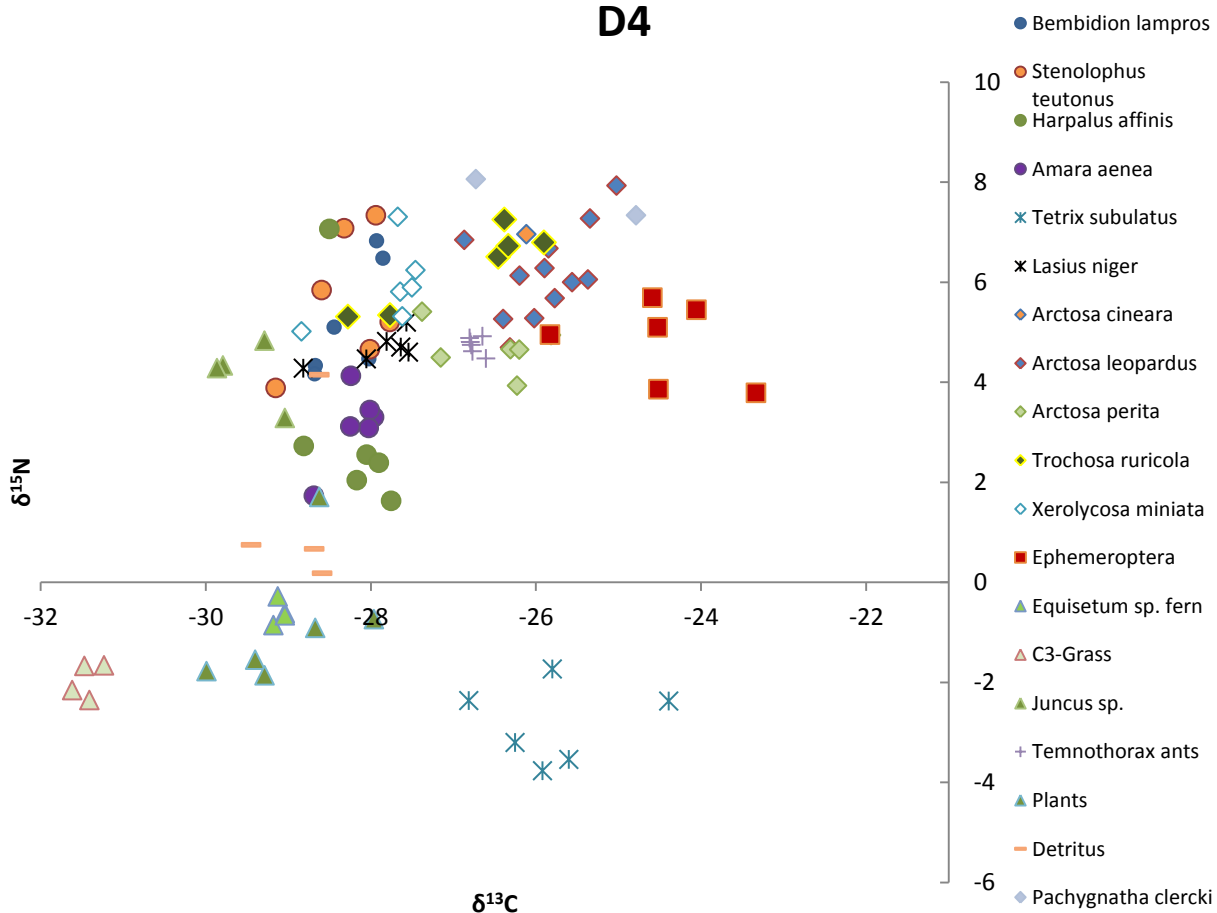
## D2



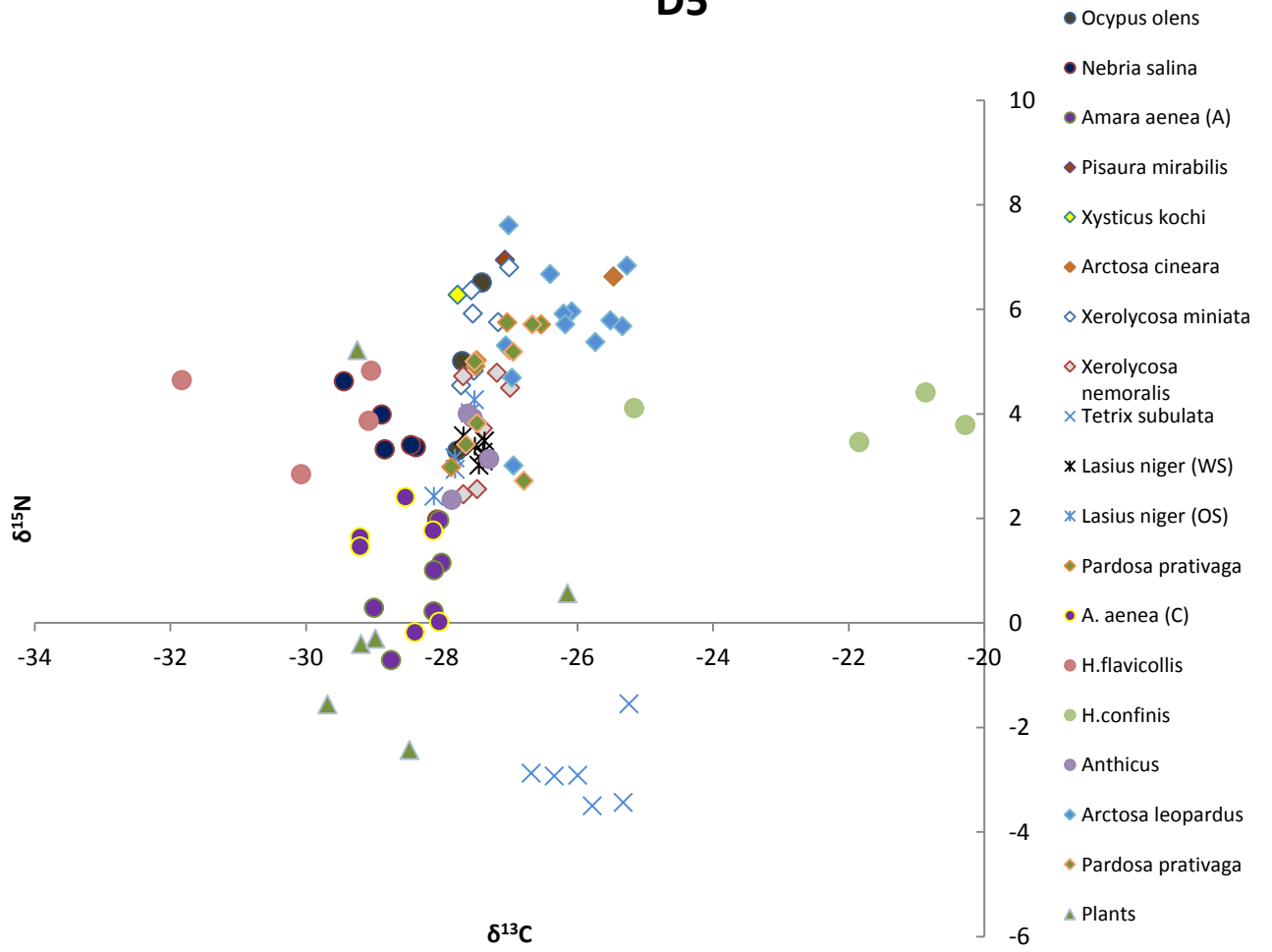
## D3



# D4

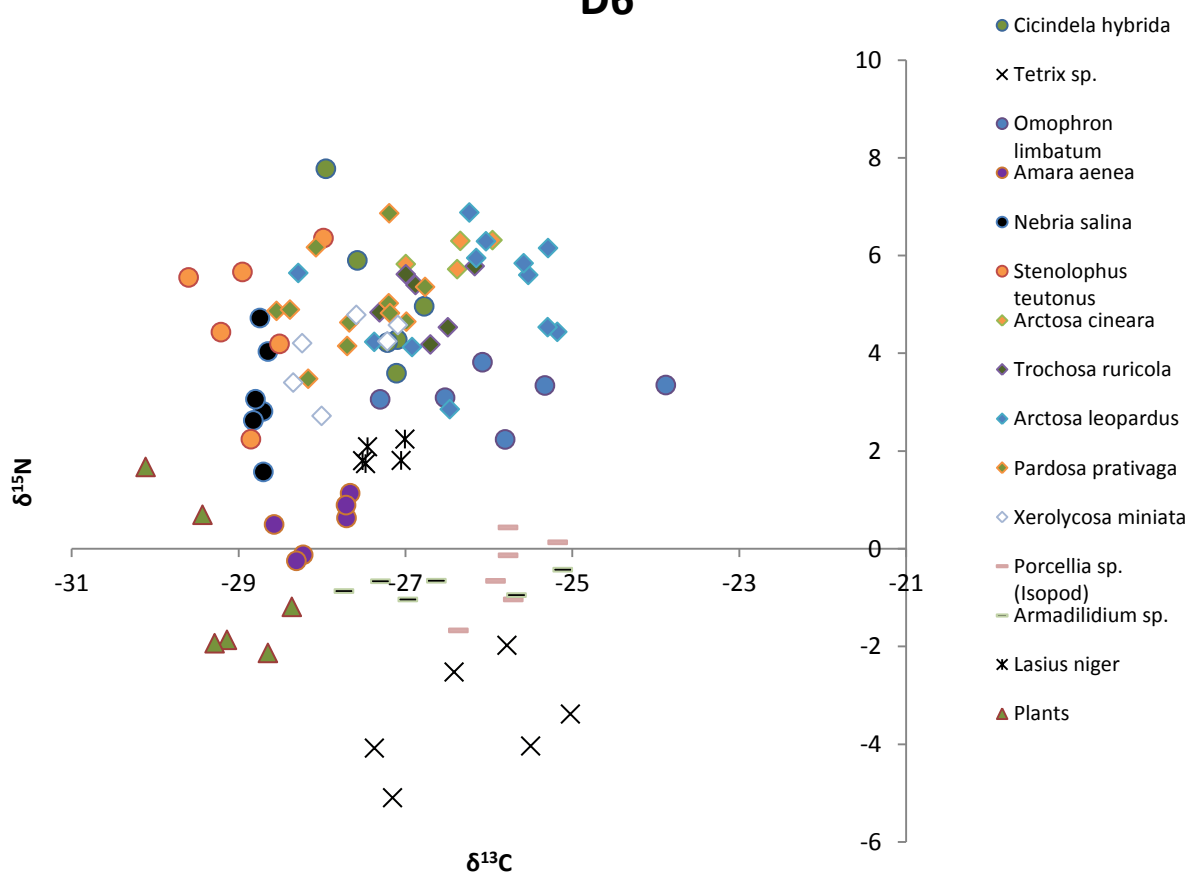


# D5

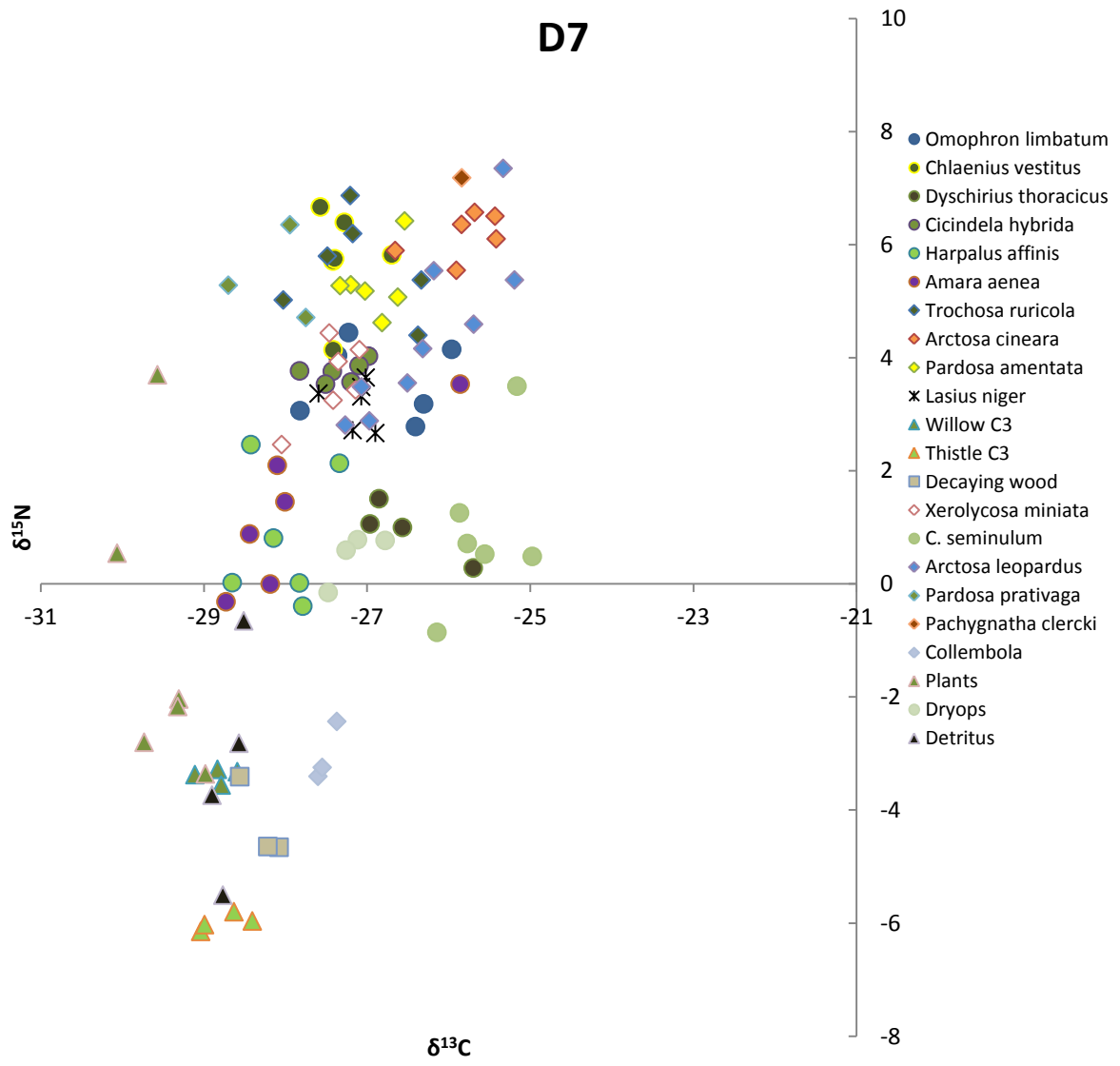




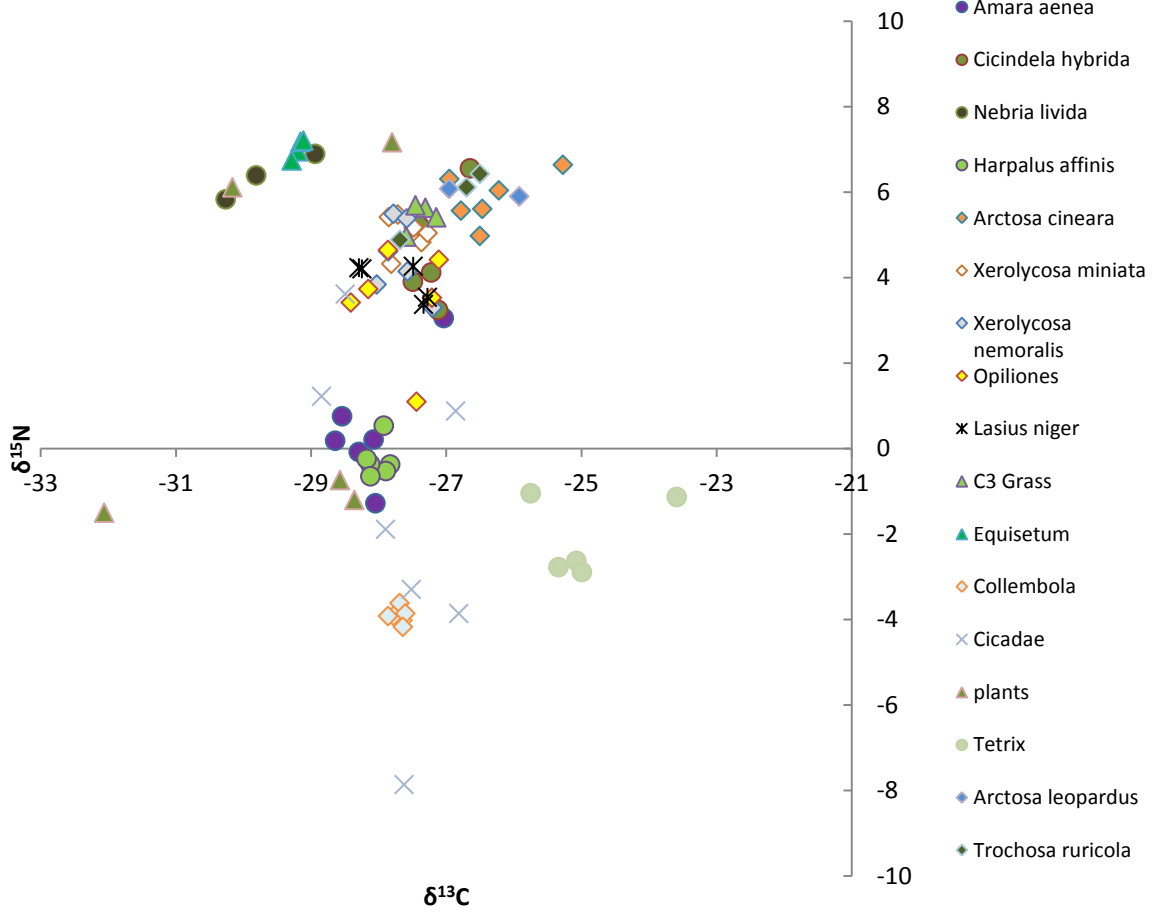
# D6



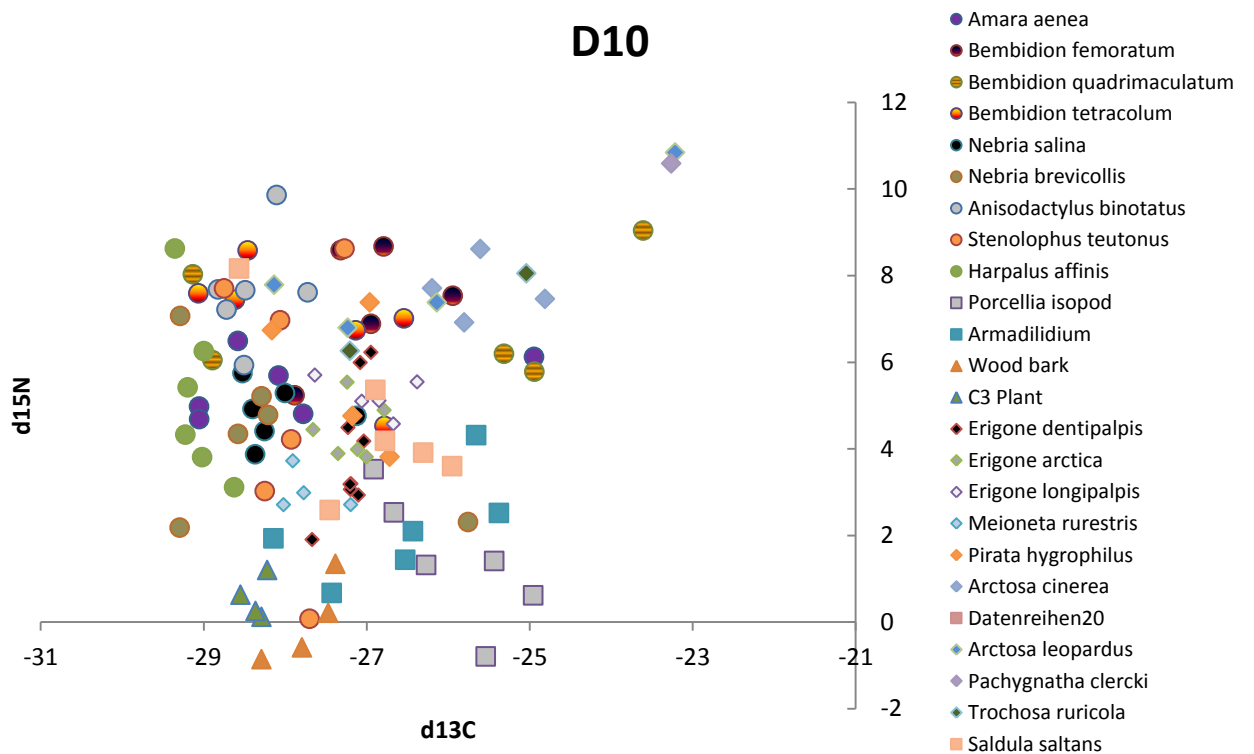
D7



### D8



### D10



"Ich, Erich Biermann, geb. am 19.06.1973 in Köln, versichere hiermit, dass ich die von mir vorgelegte Dissertation selbstständig angefertigt, die benutzten Quellen und Hilfsmittel vollständig angegeben und die Stellen der Arbeit – einschließlich Tabellen, Karten und Abbildungen –, die anderen Werken im Wortlaut oder dem Sinn nach entnommen sind, in jedem Einzelfall als Entlehnung kenntlich gemacht habe; dass diese Dissertation noch keiner anderen Fakultät oder Universität zur Prüfung vorgelegen hat; dass sie noch nicht veröffentlicht worden ist, sowie dass ich eine solche Veröffentlichung vor Abschluss des Promotionsverfahrens nicht vornehmen werde. Die Bestimmungen dieser Promotionsordnung sind mir bekannt. Die von mir vorgelegte Dissertation ist von Herrn Prof. Dr. Michael Bonkowski betreut worden."

Köln, den 05.03.2014

Erich Biermann