

**Food web ecology:
models and application to conservation**

par

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IMPRIMATUR POUR LA THESE

**Food web ecology:
models and application to conservation**

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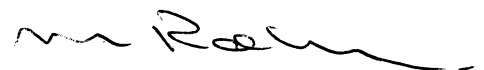
La Faculté des sciences de l'Université de
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Martine Rahier

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Foreword

The present PhD thesis of Marie-France Cattin Blandenier is part of a larger research project entitled A quantitative approach to food web ecology. This project was funded by the Swiss National Science Foundation. Two PhD students, Marie-France and Carolin Banašek-Richter, were involved in this enterprise.

What is not apparent in the present thesis is that Marie-France also participated actively in the part of the project dedicated to the development, testing and application of quantitative descriptors of food webs. She was deeply involved in the development of the quantitative food-web descriptors, which resulted in a publication in *Ecology* (Bersier L.-F., Banašek-Richter, C. & Cattin, M.-F. 2002. Quantitative descriptors of food web matrices. *Ecology*, 83: 2394-2407), and, to a lesser extent, in the testing of the robustness of these descriptors to varying degrees of sampling effort (Banašek-Richter C., Cattin, M.-F. & Bersier L.-F. 2004. Sampling effects and the robustness of quantitative and qualitative descriptors of food webs. *Journal of Theoretical Biology*, 226: 23-32). The application of these descriptors to real data should result in two publications (firstly: Banašek-Richter C., Bersier L.-F., Cattin M.-F., Merz Y., Baltensperger R., Gabriel J.-P., de Ruiter P., Tavares-Cromar A., Ulanowicz R.E., Winemiller K. Complexity in quantitative food webs. In prep. Secondly: Banašek-Richter C., Bersier L.-F. and Cattin M.-F. The structure of quantitative food webs. In prep.). Again, Marie-France was involved here not only as she assisted in the development of the descriptors, but also since one of the data sets used in both publications is that of the Grande Cariçaie (Chapter 3 of the present thesis). It must also be noted that Carolin participated actively in data collection and in the identification of many taxonomic groups of this data set.

Finally, Marie-France put a lot of time and energy in the experimental part of the research project. The aim was to test the hypothesis that the occurrence of trophic cascades is triggered by the edibility of plants. We took advantage of the fact that the wet meadows of the Grande Cariçaie are dominated by two unpalatable plants (*Schoenus nigricans* and *Cladium mariscus*). We used the palatable *Lolium perenne* to test this hypothesis. *Lolium* were planted in 24 pots (50 cm of diameter), cultivated in Neuchâtel's Botanical garden, and brought to our field site in the Grande Cariçaie. We manipulated the edibility of *Lolium* with jasmonate. We used a two factorial design with edibility of plants (edible vs. less edible) and density of spiders (high vs. low) as the controlled variables. The expected herbivores were crickets, and we had to protect the pots against roe-deer with wire netting. Unfortunately, we failed to protect the pots against voles... This huge amount of work was annihilated in a few nights by voles, which much appreciated our experiment.

Louis-Félix Bersier

I General introduction

A food web describes the feeding relationships among the organisms in an ecosystem. The key role of trophic interactions and biomass fluxes in our understanding of the functioning of ecosystems (e.g., Hairston & Hairston 1993, Paine 1988, Polis 1991, Polis & Strong 1996) explains the wide interest food-web studies encounter among ecologists. Feeding relationships are the most important interaction type between species, and the most influential on the dynamics of food webs. Different approaches to food-web ecology are possible. Topological analyses of food webs were pioneered by Cohen (1978), Pimm (1982), Sugihara et al. (1989) and Cohen et al. (1990). Detailed empirical studies of natural communities specifically aimed at describing trophic links among species were then carried out (Baird & Ulanowicz 1989, Warren 1989, Hall & Raffaelli 1991, Martinez 1991, Havens 1992, Polis 1991, Goldwasser & Roughgarden 1993). Topological and static descriptions of food webs are at the origin of generalisations resulting in the formulation of food-web models (Cohen & Newman 1985, Williams & Martinez 2000). Such static descriptions are a prerequisite to the comprehension of the dynamic structure of feeding interactions (DeAngelis 1975, Sugihara 1982, Kondoh 2003).

This thesis deals with two different aspects of food webs. The first part describes an empirical food-web study applied to the management of a site of great importance for nature conservation in Switzerland, the Grande Cariçaie (Lake of Neuchâtel, see “study site”). The second part introduces a new model of food-web structure, the nested-hierarchy model, which solves major problems of former models.

Part 1: A food web study applied to conservation

Conservation studies are typically centred on a single taxonomic group, on some indicator species or assemblages of species (e.g., Kremen 1993). Vegetation or invertebrate predators are often chosen, and two main reasons justify this choice. Firstly, invertebrate diversity is known to increase with plant structural diversity (Lawton 1983), which is generally dependent on plant species diversity. Studies of the effect of management on the vegetation should indirectly provide information on herbivore diversity and on the upper trophic levels feeding on herbivores, because parameters describing vegetation structure provide information on invertebrate species richness (e.g. Schwab et al. 2002). Secondly, studies of predatory groups (e.g., carabid beetles, spiders or Odonata) are often chosen as indicator for general impacts of management on invertebrates, because they are supposed to integrate

effects on all lower trophic levels (e.g., Maelfait & Baert 1988). Such studies are sometimes used to give indications of the changes resulting from management or other modifications affecting the whole ecosystem. These taxonomically restricted studies however do not provide direct information on the modifications affecting ecosystem organization. A food-web approach can fill this gap.

Applied food-web studies have been performed in aquatic environments. They often tackle the impact of pollutants (heavy metals such as mercury, or organochlorine contaminants) on the species in lake or marine food webs (e.g. Bowles et al. 2001, Atwell et al. 1998, Jarman et al. 1996). The accumulation of pollutants in species occurring at different trophic levels is the main focus. Such an ecotoxicologic approach however does not take into account the structural complexity of food webs, which may also be altered. Changes in the biotic and abiotic conditions of ecosystems are likely to affect food-web structure. Climatic factors and pollutants as well as conservation management practices can cause such modifications. A better comprehension of food-web structure and of ecosystem functioning is necessary for a more efficient approach to resource management and endangered species conservation (Crowder et al. 1996, Loreau et al. 2001, Thebault & Loreau 2003).

Here, we propose two different approaches to gain a deeper insight in the changes attributable to management by mowing. First, we examine the impact of mowing on the spider community of two types of wet meadows. Secondly, we construct the complete food webs of the same wet meadows to detect effects of this treatment type on food-web structure. Our study is, to our knowledge, the first analysis of food webs applied to conservation in a terrestrial environment. It tackles the static structure of food webs in wet meadows and the modifications caused by mowing in these ecosystems. An understanding of the changes in food-web structure due to mowing is an indispensable step towards the comprehension of the dynamic relations between species.

Impact of mowing on spiders –A management protocol has been implemented in the wet meadows of the Grande Cariçaie (see “study site”). It consists of a triennial winter mowing of parts of the marshes, at a maximum height of 15 cm above ground, with hay removal. Studies have been undertaken to measure the influence it has on different types of organisms. Impacts of mowing on two taxonomic groups are now well established: vegetation (e.g. Buttler 1987, 1992, Güsewell et al. 1998, Güsewell et al. 2000) and avifauna (Antoniazza & Maillefer 2001). There is however a lack of data on the effects that the present management scheme has on invertebrates. Spiders are known to be a good indicator group because of the selectivity of their ecological requirements (e.g. Clausen 1986). Moreover, their high sensitivity to vegetation and litter structure (e.g. Duffey 1966, Robinson 1981, Greenstone 1984), both strongly influenced by mowing with hay removal, makes them an

ideal candidate for such a study. The impact of mowing on the spiders of two types of wet meadows is presented in Chapter 2.

Impact of mowing on food webs – Studies on limited taxonomic groups only provide partial information on the impact of management on an ecosystem. As food-web studies allow a deeper characterization of ecosystem structure, the comparison of food webs in mown and unmanaged areas should make it possible to evaluate the impact of management on the structure and the functioning of the ecosystem. The detection of such changes is of greatest importance for the understanding of the consequences of a management practice aimed at species conservation (Crowder et al. 1996), and to be able to suggest better protocols. The impacts of mowing on the food webs of the wet meadows of the Grande Cariçaie are discussed in Chapter 3.

Study site – Two main reasons motivated the choice of the Grande Cariçaie (south shore of Lake Neuchâtel) as our study site. Firstly, it has a particularly high value for nature conservation in Switzerland and Europe (Ramsar Convention), because of its large surface and of the variety of environments represented. It extends along the 40 km of the south shore of Lake Neuchâtel and comprises reed beds, marshes (700 ha), and riparian forests (1100 ha), for a total area of more than 4000 ha, 2300 ha of which are nature reserves. The Grande Cariçaie includes 20% of the fenlands of national importance of the Swiss Plateau. Secondly, a preliminary knowledge of the organisms present is doubtlessly a strong advantage in a food-web study. This is indeed the case in the Grande Cariçaie, where various inventories have been undertaken. A synthesis concerning animal species can be found in Mulhauser (1997) and several studies dealing with the vegetation of wet meadows have been performed (e.g., Buttler 1987, Keller 1969, Roulier 1983).

These wetlands were artificially created during the first Jura waters correction (1868 - 1889), which consisted of the drainage of large areas of the Swiss Plateau and resulted in the lowering of the water level of the lakes by 2.7 m. The Grande Cariçaie acted then as a refuge for many wetlands species that would have probably otherwise become extinct. A second correction (1962 - 1973) was carried out to regulate the water level of the lakes (Buttler et al. 1985). This regulation of the water level prevented large floods, increasing brushwood encroachment and terrestrialisation. A management scheme was initiated in 1984 to obviate succession and impoverishment of the vegetation of the marshes' driest areas.

According to the Braun-Blanquet phytosociological classification, our study sites (central coordinates on the Swiss national grid: 565'500/198'950, Fig. 1) are situated in two vegetation types, namely the *Cladietum marisci* Allorge 1922 (Fig. 2) and the *Orchio-*

Schoenetum nigricantis Oberd. 1975 (Fig. 3) (Buttler & Gallandat 1990), both in mown and unmanaged conditions. The first association is found on frequently inundated soils and is nearly completely dominated by *Cladium mariscus*. The ability of this species to grow with almost no interruption gives this association a high competitive potential, which permits it to invade the adjacent vegetation. *Schoenus nigricans* and some rare orchid species, *Orchis palustris* and *Spiranthes aestivalis*, characterise the second association. Brushwood encroachment is especially rapid in this relatively dry part of the marshes and threatens these rare species. Management by mowing in these meadows is intended to reduce the vitality of *Cladium mariscus* in the first association and to preserve botanical diversity in the second association (Buttler 1987). A control area has been kept unmanaged since winter 1991 – 1992 for monitoring purposes.

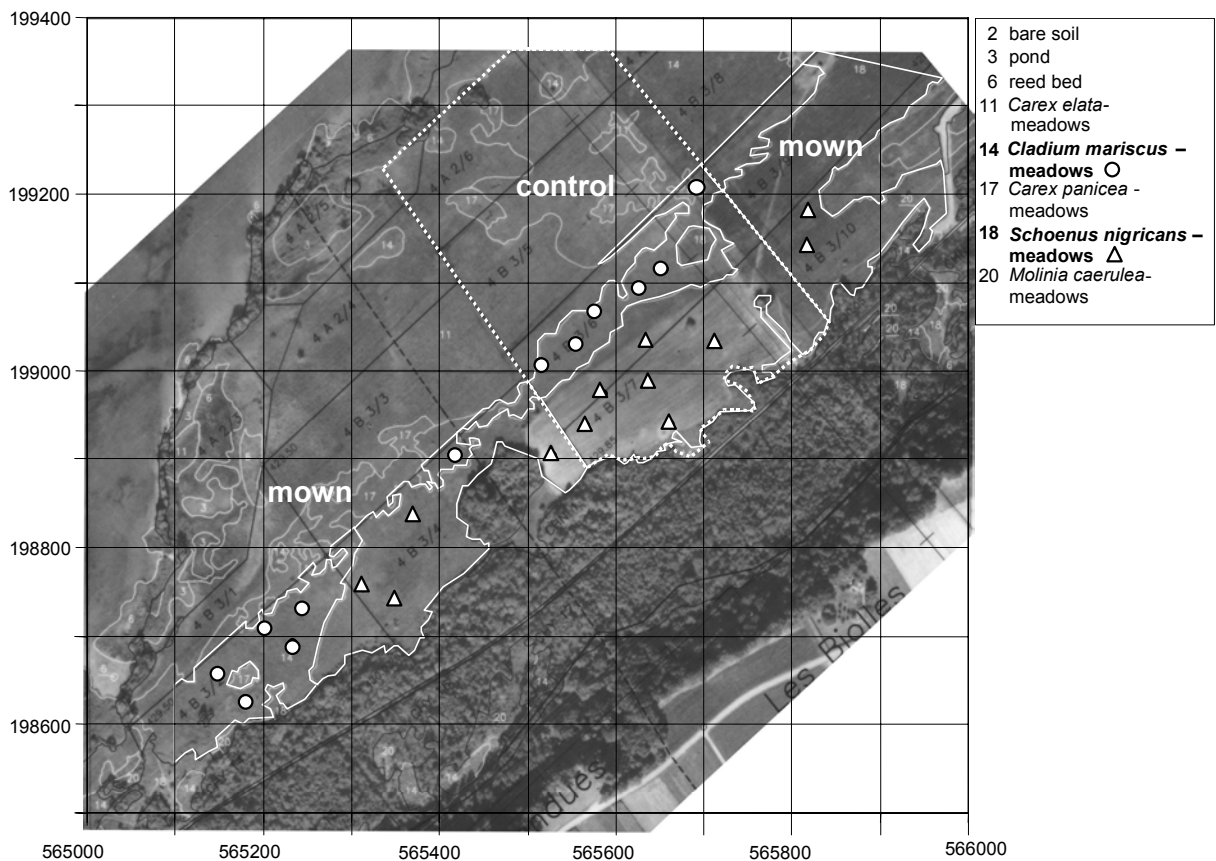


Fig. 1. Aerial photography of the study site, with Swiss coordinates (Swisstopo 1994). Dots show the location of the cores (see Method section in Chapt. III).

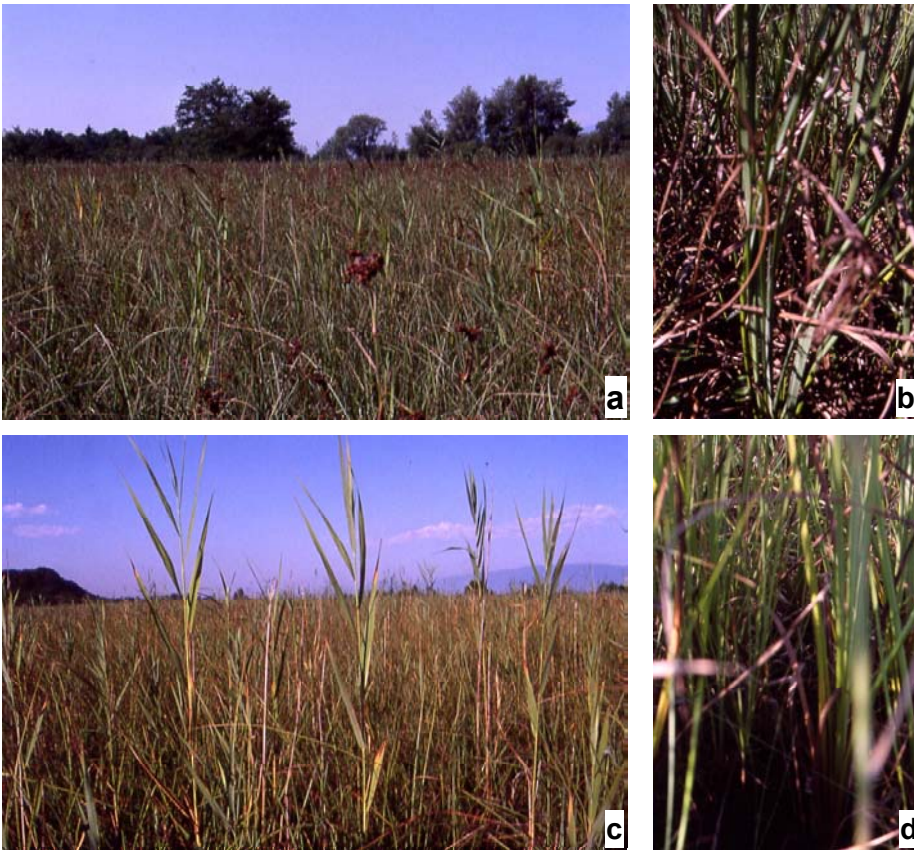


Fig. 2.
Cladietum marisci.
(a,b) control
(c,d) mown

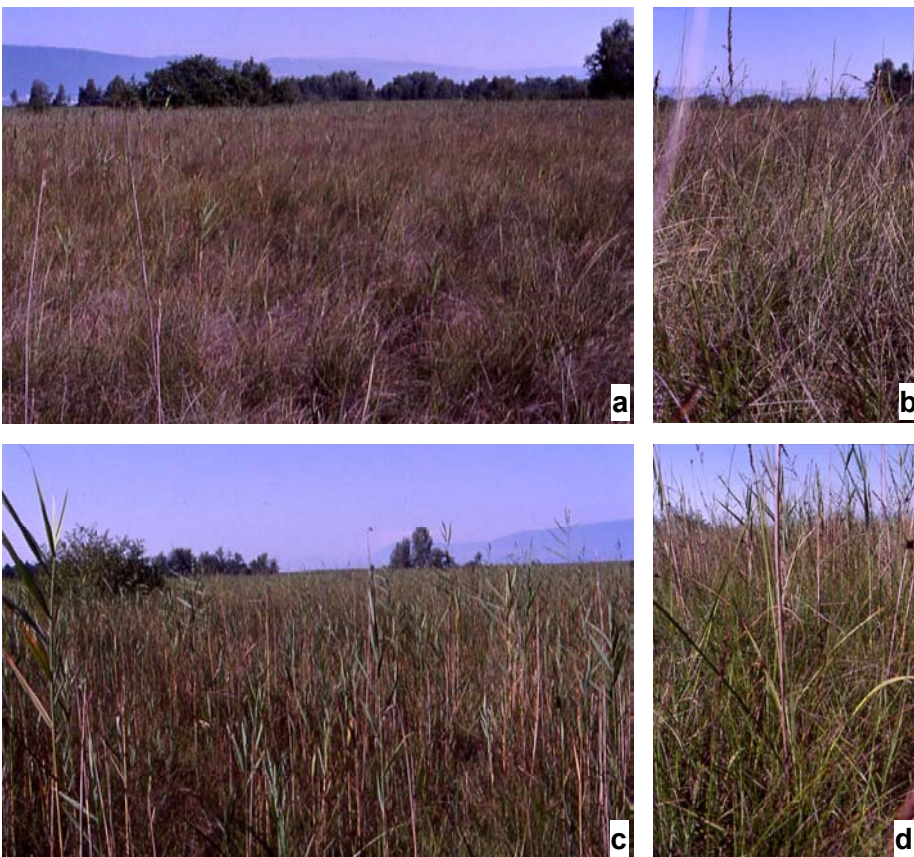


Fig. 3.
Orchio-Schoenetum nigricantis.
(a,b) control
(c,d) mown

Part 2: Food-web models

Food-web properties and regularities – Food webs are complex objects, and simple and ecologically meaningful properties have been proposed to synthesize the information contained in these topological descriptions of communities. Examples of such properties are the fraction of basal species (species without prey), of top species (species without consumer), of intermediate species (species with both prey and consumers) or the linkage density (total number of links divided by the number of species). A comparison of various properties among collections of community food webs was performed and regularities were observed (Cohen 1977, 1989, Pimm 1982, Briand & Cohen 1984, Lawton 1989, Sugihara et al. 1989, Pimm et al. 1991, Havens 1992). Among these generalities, the proportions of top, intermediate and basal species were found to be constant when species number in the web varies. The observation of regularities fostered the formulation of models explaining food-web structure.

Cascade model and niche model - In the cascade model (Cohen & Newman 1985), species are ranked from 1 to S (total number of species), and a consumer can only prey on species of lower rank. The ranking of the species was hypothesized to be a body size ordering (Lawton & Warren 1988). It was found to reproduce the properties seen in early collections of food webs. The quality of the data on which this model was based was however criticised (e.g. May 1983, Paine 1988). These criticisms include the poor resolution of the taxa, a bias towards more aggregation for basal species, and the differences between authors in the criteria for the attribution of trophic links. A strong effort was then made to collect data specifically to describe the feeding relationships in communities (Baird & Ulanowicz 1989, Warren 1989, Hall & Raffaelli 1991, Martinez 1991, Havens 1992, Polis 1991, Goldwasser & Roughgarden 1993, Deb 1995). These detailed descriptions of food webs from terrestrial and aquatic environments did not confirm the previously found regularities and, unsurprisingly, the cascade model failed to properly describe these high-quality food webs.

Williams & Martinez (2000) proposed a new model, the niche model, which can be viewed as an extension of the cascade model, and which predicted very precisely some properties of the highest-quality data available. The niche model ranks the species according to a randomly drawn “niche value”. A consumer eats all species falling into a range, which restricts diets to be continuous. Contiguity reflects the ecological assumption that diets can be arranged along one niche dimension. Some important features of food webs are however not taken in account with this approach. Firstly, the niche model is known to produce only interval food webs. These interval food webs possess the characteristic that the feeding relationships between consumers can be represented in one dimension (Cohen 1978, Pimm

1982), thought, as for the cascade model, to correspond to a body size hierarchy. However, non-interval food webs characterise the highest-quality dataset available (Williams & Martinez 2000). Secondly, a key assumption of the niche model, contiguity of diets, is not observed in real food webs.

What determines feeding relationships between species is the central question at the origin of the proposition of food-web models. Former hypotheses will now be briefly compared with the features observed in the eight matrices sampled in the Grande Cariçãie wet meadows. May (1974) hypothesized trophic links to be randomly distributed among species. A simple visual inspection of the eight food webs we described in the Grande Cariçãie is sufficient to eliminate this idea, as links are clearly aggregated in blocks. The cascade model postulates species to be ranked according to the size of the species, and rejects cannibalism. Our data set shows that cannibalistic links are indeed present, and that exceptions to the rule that consumers prey only on smaller prey are not rare, for example among spiders. Thomisidae and Philodromidae, or web building spiders for example frequently catch prey larger than their own size. Moreover, our food web matrices are not upper triangular. Finally, the niche model postulates no gaps in diets and species to be ordered along a single niche dimension. We computed the probability that an irreducible gap exists in our food webs (Disdiet), and found values different from zero.

These observations encouraged us to think again at the mechanisms behind trophic links. A connection between taxonomic similarity and trophic similarity is put in evidence in our data by the block structure of the feeding links. We are aware that it is partially the result of the construction of the matrix, based on literature data, but the same connection can also be observed in matrices based only on empirical data (see Chapter 4). The presence of all feeding links can however not be explained by this connection and innovation has also a role in diets. We propose here a simple rule for the construction of food webs based on the idea that both phylogenetic constraints and adaptation determine food-web structure.

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II The impact of mowing as a management strategy for wet meadows on spider (Araneae) communities¹

1. Introduction

Mowing is a widely used management technique for meadows, either in pursuit of agricultural interests or for nature conservation. Several studies have been carried out to assess the effect of mowing on vegetation, often showing positive effects on floristic diversity: e.g. Cowie et al. (1992) on reed bed vegetation, Buttler (1992) and Gusewell et al. (1998) on calcareous fen vegetation. For arthropods, mixed, and in some cases negative effects of mowing on the fauna of different grassland types have been found (Gerstmeier and Lang 1996). Dithogo et al. (1992) studied the effect of mowing and burning on different groups of arthropods in reed beds, and found short-term effects, but no major influence on the invertebrate community after one year of management. In a study on the effect of mowing on arthropods in wet meadows, Klieber et al. (1995) found that no species were favoured by mowing. Pozzi et al. (1998) recommend practicing a very extensive mowing regime to keep valuable spider communities in dry meadows. Decler (1990) found evidence for a negative effect of cutting on rare and some widespread wetland spider species and a positive effect on ubiquitous ones in reed marsh vegetation. A review of management effects on spider communities in grassland can be found in Bell et al. (2001).

The Grande Cariçaie, located at the south shore of Lake Neuchâtel (Switzerland), is a site of international importance for nature conservation (Ramsar Convention). Its marshes are mown once every three years to prevent succession. Given the few existing studies on the effect of mowing on spiders in wetlands, and the discrepant results found for other groups of arthropods, an efficient management scheme requires precise knowledge of the consequences of mowing on this group. Consequently, the present study focuses on the effect of mowing on spiders in two different types of fen meadows located at the south shore of Lake Neuchâtel. Differences between vegetation and treatment types are examined for spider density, spider repartition among families and diversity measures. Characteristic taxa are also determined for each vegetation and treatment type and management suggestions are provided. Studies on the effect

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of mowing on the vegetation (e.g. Buttler 1987; 1992; Güsewell et al. 1998; Güsewell et al. 2000), and nesting birds (Antoniazza and Maillefer 2001) have already been carried out at this location, but there is a need for a closer look at its effects on arthropods. Spiders should be a good indicator group for this purpose, because of their sensitivity to the vegetation and litter structure (e.g. Duffey 1966; 1975; Uetz 1979; Hatley and Macmahon 1980; Robinson 1981; Greenstone 1984; Luff and Rushton 1989; Gibson et al. 1992), which are strongly influenced by mowing with hay removal. Several authors (e.g. Clausen 1986; Maelfait and Baert 1988; Villepoux 1991; Marc et al. 1999) point out the selectivity of spiders' ecological requirements thus enhancing their high potential for bioindication.

2. Study site

The Grande Cariçaie is a complex of reed beds, marshes, and riparian forests, extending along the 40 km of the south shore of Lake Neuchâtel, over more than 4000 ha, 2300 ha of which is protected as a nature reserve. It was created artificially during the first Jura waters correction (1868 - 1889), which consisted of drainage of large areas of wetlands and a lowering of the water level by 2.7 m. A second correction was carried out between 1962 and 1973 to regulate the water level of the lake (Buttler et al. 1985). These large-scale modifications of the western part of the Swiss Plateau landscape resulted in the drying of large areas formerly covered with wetlands. The Grande Cariçaie consequently acted as a refuge for many stenotopic species typical of these environments. The high diversity of habitats within this site probably makes of it one of the richest in the country with respect to species number: more than 3500 animal species were found in a recent survey (Mulhauser 1997). The lowering of the water level however resulted in an increasing brushwood encroachment and succession followed by an impoverishment of the vegetation of the driest areas of the marshes. A management scheme including triennial winter mowing of parts of these marshes, at a maximum height of 15 cm above ground, with hay removal, was initiated in 1984 to prevent these effects.

Vegetation types are typically distributed in belts depending on the distance from the lake. According to the Braun-Blanquet phytosociological classification, our study sites (central coordinates on the Swiss national grid: 565'500/198'950, Fig. 1) comprise two vegetation types; the *Cladietum marisci* Allorge 1922 (hereafter, *Cladietum*) and the *Orchio-Schoenetum nigricantis* Oberd. 1975 (hereafter, *Schoenetum*) (Buttler and Gallandat 1990). The first association is to be found on frequently inundated soils and is nearly completely dominated by *Cladium mariscus*. The capacity of this species to grow with almost no interruption gives this association a high competitive potential, which enables it to invade the adjacent vegetation. The

second association comprises *Schoenus nigricans* and some rare orchid species, *Orchis palustris* and *Spiranthes aestivalis*, Brushwood encroachment is especially rapid in this drier part of the marshes. The main goals of the management of these areas by mowing (Buttler 1987) are to reduce the vitality of *Cladium mariscus* in the first association and preserve the botanical diversity in the second. A control area has, however, been kept unmanaged since at least winter 1991 – 1992 for monitoring purposes. The managed part of the study area was last mown in March 1999.

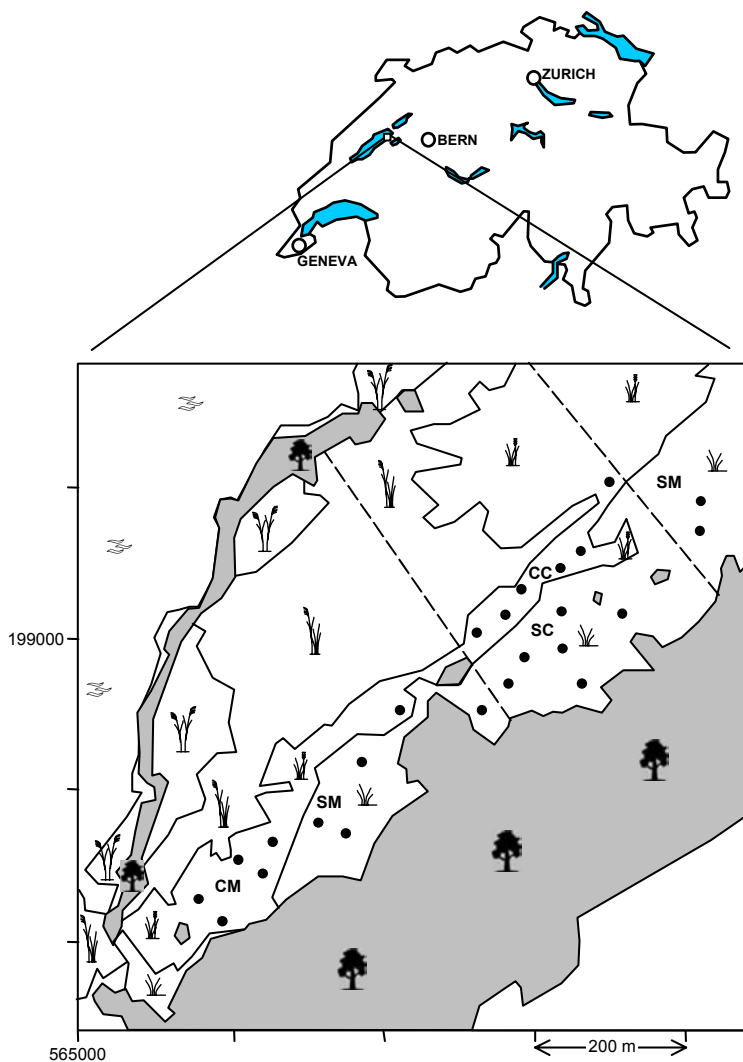


Fig. 1. Location of the study plots, in two vegetation types, mown triennially or unmanaged (control). CC : *Cladietum marisci*, control; CM : *Cladietum marisci*, mown; SC : *Orchio-Schoenetum nigricantis*, control; SM : *Orchio-Schoenetum nigricantis*, mown. Coordinates follow Swiss national grid. Dots indicate location of the cores. The control sector is delimited by broken lines.

3. Methods

3.1. Sampling

We randomly chose 24 plots at least 20 m apart, which were sampled during two periods, from May 24th to July 21st and from August 21st to September 8th 2000. A stratified sampling design was applied, with six plots sampled in each vegetation and treatment type: i.e. *Cladietum*-mown (CM), *Cladietum*-control (CC), *Schoenetum*-mown (SM) and *Schoenetum*-control (SC). Spiders were sampled in each plot with cores measuring 50 cm diameter (~0.2 m²) and dug 20 cm deep in the soil, and by carefully collecting along transects 20 m long and 1 m wide. The cores were hand-sorted, always by the same team, to ensure constant efficiency. The spiders were then stored in 70% methanol and adults identified to species and immatures to family or genus level (and sometimes to species if unequivocal or regionally monospecific taxa). This resulted in two data sets, one for spiders collected in cores (core taxa matrix), and one for transects (transect taxa matrix). We constructed a species accumulation curve (Colwell and Coddington 1994) to check that the cumulative number of taxa reached an asymptote. This was indeed the case, which indicates an adequate sampling effort.

The vegetation of each core was cut and weighed in the fresh and the dry state. Litter depth was measured and its quantity was fresh and dry weighed. The number of living and dead reed stems (*Phragmites australis*) was also determined along transects of 50 m long and 1 m wide. The nomenclature follows Platnick (1997) for spiders and Lauber and Wagner (1996) for plant species.

3.2. Analyses

Linear spatial autocorrelation of the sites was considered, given that different vegetation types are distributed in belts depending on the distance from the lake. To test this hypothesis, a Mantel test was performed between a matrix based on the Steinhaus similarity index transformed into distances (Legendre and Legendre 1998), computed on core taxa abundances, and a distance matrix based on the Euclidian distance between the sites' spatial coordinates. These operations were performed using the "R" package of Legendre and Vaudor (1991). Since there is only one area covered with control vegetation, aggregation of stations with the same treatment is another possible reason for sites to be spatially autocorrelated (see Fig 1). To verify this hypothesis, two Canonical Correspondence Analysis (CCA) were carried out on the core taxa matrix, on mown and control plots separately, using a polynomial of the centred spatial coordinates of the cores $[\hat{z} = b_1x + b_2y + b_3x^2 + b_4xy + b_5y^2 + b_6x^3 + b_7x^2y + b_8xy^2 + b_9y^3]$ as explanatory variables (Legendre 1990; Borcard et al. 1992). The CANOCO procedure of

“forward selection of the explanatory variables” was applied (ter Braak 1988), and only significant environmental variables were retained in the analyses.

Mann-Whitney tests were used (Sokal and Rohlf 1995) to test for differences in environmental characteristics between vegetation and treatment types. Since most of the spiders captured were active on the ground, differences in some litter and ground characteristics were examined: litter density (litter dry weight/(surface x mean height)), and litter and mosses dry weight. Differences in dry and fresh reed numbers between vegetation transects were also tested.

A classification of spiders into valuation categories adapted from Decler (1990) was adopted, based on the knowledge of the Swiss (Maurer and Hänggi 1990) and European (Hänggi et al. 1995) fauna (Appendix). This classification, applied only to individuals determined to species level, is the following:

- 1) Ubiquitous species (UB), occurring in various, mostly open habitats,
- 2) Species associated with wetlands but also other mostly open habitat types (WO),
- 3) Widespread wetland species (WW) strictly preferring wet habitats,
- 4) Rare wetland species (RW), recorded fewer than 10 times until 1990 in Switzerland and strictly linked to wetlands,
- 5) Other rare species (RO), recorded fewer than 10 times until 1990 in Switzerland, living in wetlands and other habitats.

Since the four vegetation and treatment types were sampled with the same effort, a comparison between diversity indices for the cores appears sensible. We chose the following diversity and evenness measures: (1) the minimum number of species in a sample, estimated by counting immatures and other supraspecific taxa as additional species only if no similar species was present in a sample (Gibson et al. 1992), (2) the number of taxa in a sample (S), (3) the reciprocal of Shannon diversity (the diversity number of Hill 1973):

$$DN = e^H, \text{ with } H = -\sum_{i=1}^S p_i \cdot \ln p_i, \text{ where } p_i \text{ is the relative abundance of the } i^{\text{th}} \text{ species, and (4)}$$

Hurlbert's (1971) probability of an interspecific encounter :

$$PIE = \left(\frac{N}{N-1} \right) \cdot \left(1 - \sum_{i=1}^S \left(\frac{m_i}{N} \right)^2 \right), \text{ with } N \text{ the total number of individuals, and } m_i \text{ the number of}$$

individuals of species i .

In order to evaluate differences between vegetation and treatment types for diversity measures, numbers for the most abundant spider families and for valuation categories, the two-tailed Mann-Whitney non-parametric test was applied. When two tests were performed simultaneously on the same data, Holm's correction (1979) was used. Only families with on average at least one individual found in each sampling unit are taken into account.

The IndVal method (Dufrêne and Legendre 1997) was used to determine the characteristic taxa of each vegetation and treatment type. This method computes "indicator values" (hereafter IndVal) for every taxon. These IndVal indices range from 0 to 100 and reach their maximum for a taxon whose individuals are all present in a single group of plots and if the taxon is present in all plots of this group. Furthermore, these values can be tested for significance using permutations that randomly reallocate plots among plot groups. For the CCA and the IndVal analysis, taxa with less than three occurrences were deleted and taxa abundances were log-transformed [$m_i' = \ln(m_i + 1)$]. Very young spiders, i.e. immatures of Lycosidae on the females' backs or of the first instar of *Larinioides* sp. in their web, were also deleted for all analysis to avoid a distortion of our data.

4. Results

4.1. Spatial autocorrelation

The Mantel test performed on the similarity matrices based on the core abundances of the taxa and the spatial coordinates was significant ($P = 0.04$), indicating that our sites were linearly spatially autocorrelated. This spatial structure may however simply be due to the adjacent location of control and mown areas (see Fig. 1). To evaluate this possibility, we performed a CCA separately for each group of plots. If the observed spatial autocorrelation is due simply to the location of the control and mown areas, we expect not to find evidence of spatial structure for plots within each group. This was indeed the case for the control plots, where no spatial structure was revealed, since no term of the polynomial of the centred spatial coordinates was found significant. There were, however, significant terms for the mown plots, indicating a spatial structure. Since we cannot obviously change anything in the mown and control plots repartition, we have to interpret marginally significant results carefully.

4.2. Environmental descriptors

The results of the Mann-Whitney tests showed that there was a highly significant difference in litter dry weight between vegetation types, litter being greater in the *Cladietum* (Table 1). Biomass of mosses was significantly greater in the mown areas, and number of dry

reed stems significantly lower. Neither treatment nor vegetation significantly influenced litter density.

Table 1. Treatment and vegetation effects on environmental descriptors. Median and results of Mann-Whitney tests (U and Holm-corrected *P*-value, * indicates a significant result).

	Treatment				Vegetation			
	Mown	Control	U	<i>P</i>	<i>Cladietum</i>	<i>Schoenetum</i>	U	<i>P</i>
Litter dry weight in cores (g)	314	422	51	0.225	461	258	5	0.001*
Moss dry weight in cores (g)	28	7	27	0.018*	8	22	43	0.094
Litter density in cores (kg/m ³)	2.83	3.92	55	0.326	4.15	3.66	43	0.188
Dry reed number (transects)	44	235	0	0.008*	98	168	12	0.337
Fresh reed number (transects)	79	139	7	0.156	140	97	8	0.109

4.3. Diversity and abundance of spiders

We collected 2547 individuals, belonging to 17 families and 53 species. Most individuals were juveniles but 237 adults were sampled of which 15.2% were males. The mean density determined on the basis of core samples was approximately 250 individuals/m².

Vegetation influenced spider density significantly, *Cladietum* being significantly richer than *Schoenetum* for both cores and transects (Mann-Whitney two-tailed test, *P* = 0.018 and 0.014, respectively). However, no significant differences could be found for any diversity measure. For core data, the Mann-Whitney test revealed significant differences for the abundances of the families Linyphiidae (*P* = 0.014), Lycosidae (*P* = 0.032), Clubionidae (*P* = 0.027) and Salticidae (*P* = 0.024). Unlike the Salticidae, Lycosidae and Linyphiidae both showed a preference for *Cladietum*. For spiders collected along transects, vegetation had a significant effect on Linyphiidae (*P* = 0.018) and to a lesser extent on Araneidae (*P* = 0.056), both showing a preference for *Cladietum*.

In the second growing season after mowing, we found no treatment effect on spider density (Tables 2, 3), nor on any diversity measure. For core data (Table 2), the Hahniidae and Clubionidae were negatively affected by mowing, with a significant reduction in numbers in the managed plots. In cores, no effect of treatment could be found for the Linyphiidae, Lycosidae, Salticidae, and Philodromidae. For transect data, mowing had no significant effect on any family (Table 3). When grouping species according to valuation categories (see Appendix), the Mann-Whitney tests revealed a significant positive effect of mowing on WO species, and a negative effect on RO species (Table 4). No significant effect of mowing was found for the other groups.

Table 2. Treatment effects on diversity and number of spiders in cores. Median and results of Mann-Whitney tests (U and Holm-corrected *P*-value, * indicates a significant result). PIE : probability of an interspecific encounter.

	Mown	Control	U	<i>P</i>
Minimum number of species	10	10	60.5	0.499
Number of taxa	12.5	12.5	62.5	0.581
Inverse of Shannon diversity	1.84	2.03	52	0.248
PIE	0.77	0.82	51	0.45
Number of spiders :				
All taxa	45	45.5	65.5	0.707
Linyphiidae	21	16	68	0.795
Lycosidae	16	14.5	63	0.603
Hahniidae	1.5	4	30	0.026*
Clubionidae	1	3	34	0.050*
Salticidae	1	1	61	0.498
Philodromidae	0.5	1	51	0.398

Table 3. Treatment effects on number of spiders in transects. Median and results of Mann-Whitney tests (U and Holm-corrected *P*-value).

	Mown	Control	U	<i>P</i>
All taxa	40.5	35.5	62	0.564
Linyphiidae	0.5	1	66	0.691
Lycosidae	2	0.5	37	0.072
Araneidae	21.5	20	68	0.817
Salticidae	1	2.5	53	0.262
Tetragnathidae	1	0.5	45	0.204
Pisauridae	3	1	52	0.456
Philodromidae	3.5	2	48	0.3

Table 4. Treatment effects on valuation categories. Median and results of Mann-Whitney tests (U and Holm-corrected *P*-value, * indicates a significant result). UB : ubiquitous species; WO : species associated with wetlands but also other mostly open habitat types; WW : widespread wetland species; RW : rare wetland species; RO : rare species living in wetlands and other habitats.

	Mown	Control	U	<i>P</i>
UB	1	0.5	60.5	0.486
WO	3.5	1	36	0.035*
WW	3	3	57	0.382
RW	1.5	2	62	0.554
RO	0	1	34.5	0.018*

4.4. Indicator taxa

The results obtained separately for cores and transects with the IndVal method to identify characteristic taxa for both *Cladietum* and *Schoenetum* and for the four vegetation and treatment groups (CC, CM, SC and SM) are shown in Fig. 2. This method revealed indicator taxa for both the *Cladietum* and the *Schoenetum*. At the next dichotomy, the mown and control versions of both vegetation types (CM - CC and SM - SC) were also significantly characterised by some taxa. Thus, despite the fact that we found no effects of mowing on diversity measures, specific taxa appeared to respond to this treatment.

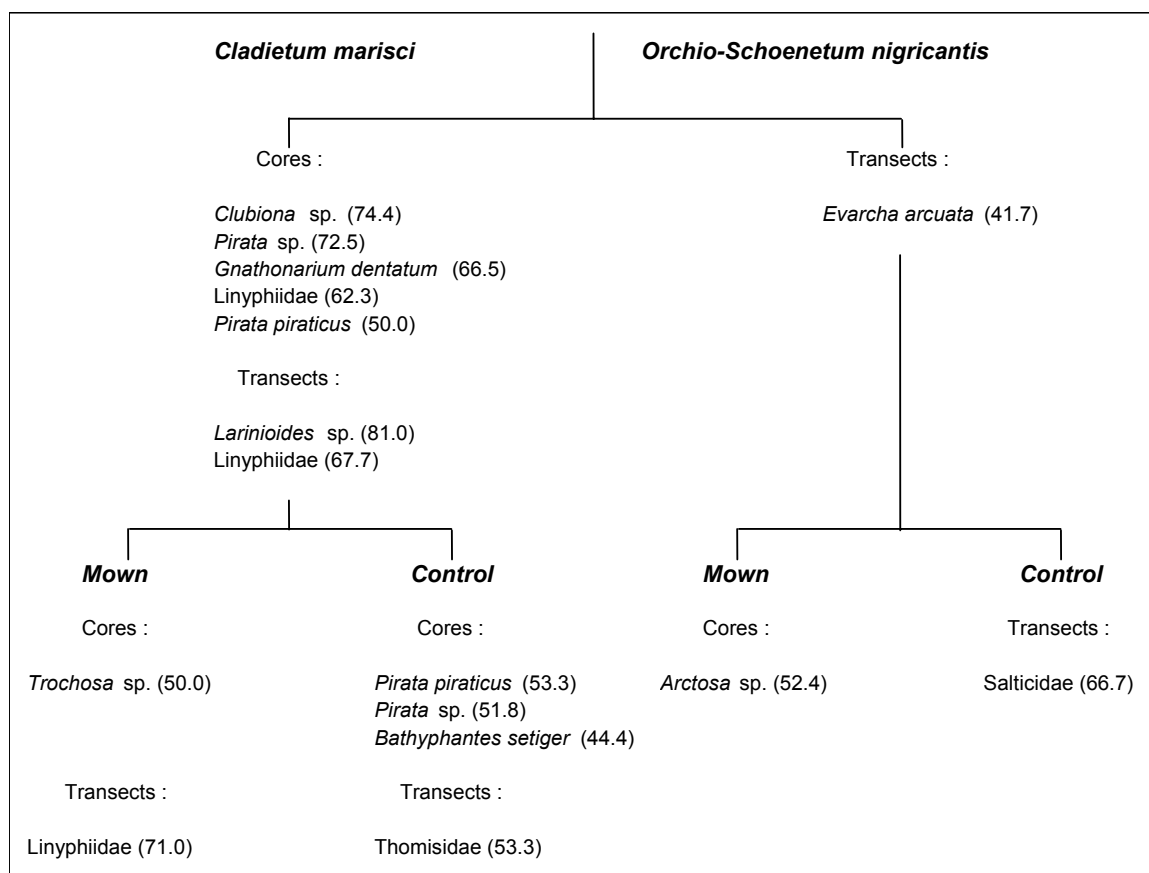


Fig. 2. Dendrogram showing the different groups and their characteristic taxa. Number in brackets are IndVal indices. Only significant taxa are presented. Cores and transects refer to both sampling methods used.

5. Discussion

5.1. Sampling methods

Sampling by cores is rarely used in ecological field studies on spiders, but allows the determination of “absolute” spider densities and gives a different picture of the spider community, compared to pitfall traps. Pitfall traps are traditionally used to catch ground and litter dwelling spiders, but with this method density depends on the mobility of individuals. The mean density found in our cores is high (250 individuals/m²) compared to densities typically found in natural and cultivated environments (50–150 individuals/m², Marc et al. 1999). Only 9.3% of the spiders we caught were adults, which is very low compared to pitfall trap values, the latter ranging around 60-70% (Hänggi and Maurer 1982; Brunhes and Villepoux, unpub.). The proportion of males we discovered is also very unusual: among adults, only 15.2% were males, with little variation across sampling periods. Hänggi (1987) caught 72.5% males and Hänggi and Maurer (1982) 62.3% using pitfall traps. The sex ratio was very surprising and further studies could be useful to explain the great imbalance between the number of males and females. There are several possible explanations, one of them being the sampling time (two separate relatively short periods) that might have impeded the capture of males if they have short life spans. Other explanations could be that there were fewer males, because each individual male mates with several females, or that males are exposed to an increased mortality rate due to a higher predation associated with their greater mobility.

Although sorting the samples is very time consuming, the core sampling method is well adapted for accurate estimations of species diversity and density. This method also provides precise indications about the species ecological requirements because they are caught at the exact place where they live. The small proportion of adult spiders collected, however, made it impossible to determine all individuals to the species level, which renders the ecological interpretation of the results slightly more difficult.

5.2. Differences between vegetation types

The vegetation type was an important factor for the differentiation of spider communities. The *Cladietum*, the vegetation growing on the wetter soils, had a significantly greater spider density than the *Schoenetum*. Consistently, Kajak et al. (2000) found a positive correlation between soil moisture and spider density. A higher litter quantity was also found in the *Cladietum*, increasing the number of available niches and consequently allowing for a greater spider density.

Mann-Whitney tests for the families based on core samples showed that Lycosidae, Linyphiidae and Clubionidae preferred *Cladietum*, but the reverse was found with the Salticidae. Most Lycosidae were immatures of *Pirata* sp., a generally hygrophilous genus (Hänggi et al. 1995). For spiders collected along transects, the vegetation had a significant effect on Linyphiidae. Species of this family preferred the *Cladietum*, probably because of its litter structure, which provides space for web building. The Araneidae showed the same preference. This can be explained by the fact that Araneidae were mostly represented by young individuals of the first instars of *Larinioides* sp., which use the *Cladium mariscus* inflorescence as shelter and support for the construction of webs.

The IndVal analysis showed that some taxa have both a high specificity and fidelity within the *Cladietum*. *Gnathonarium dentatum* and *Pirata piraticus* being both strictly hygrophilous (Hänggi et al. 1995), it was not surprising to find them as characteristic species of this often-inundated vegetation type. The adults of *Pirata piraticus* are found in small areas of open water, which frequently occur within the *Cladietum* sites. The presence of Linyphiidae immatures as an indicator taxon for this kind of vegetation in both cores and transects was consistent with the result of the Mann-Whitney test performed at the family level on core samples. The strong affinity that immatures of the *Larinioides* showed for the *Cladietum* was consistent with the result of the Mann-Whitney test performed for the family Araneidae from transects samples. The same reasoning applies for *Pirata* immatures and the family Lycosidae from core samples. The taxon *Clubiona* sp. was also characteristic of *Cladietum*, probably favoured by the abundance of vertical structures provided by the stems of *Cladium mariscus* and reed.

There were only very few indicator species for *Schoenetum*. However, Mulhauser (1989), although using different sampling and analytical methods, also did not find any characteristic spider species for this association. This relative poverty in characteristic species can be explained by the ecological properties of this vegetation type, which occupies an intermediate, sometimes inundated, environment that also undergoes dry periods. These fluctuating conditions of the abiotic environment are not a favourable setting for a species ecological optimum. The only characteristic species of the *Schoenetum* was *Evarcha arcuata*, a heliophilous species that is not strictly confined to wetlands, but prefers a habitat structure made of warm and only moderately high herbs. It is further worthwhile mentioning that *Robertus insignis*, a very rare wetland species (with few records from Europe) was almost only present (seven among nine individuals) in both control and mown plots of the *Schoenetum*.

5.3. Effect of mowing on spider community

Members of the Hahniidae and Clubionidae were reduced by mowing. The decrease in the number of Clubionidae can be related to the great diminution of the number of dry reed stems in the mown areas. These are structures used by some Clubionidae species, in particular to overwinter. Winter mowing is then particularly harmful for this group, because of the direct destruction of both the individuals and their shelter, making recolonisation after management difficult. The negative effect on Hahniidae (i.e. *Antistea elegans* except for one individual) is probably explained by the changes in litter quantity and soil surface structure due to mowing. *Antistea elegans* builds its web in small depressions in the ground, which are probably destroyed by the mowing machine, inhibiting the return of this species. Furthermore, Clubionidae are not commonly caught in studies on ballooning (Blandenier and Fürst 1998), suggesting that these spiders have a low ability for long-distance recolonisation. Hahniidae have also very rarely been cited in such studies (e.g. Dean and Sterling 1985). This fact could explain a longer recolonisation time than for other spiders using a habitat similar to that of Hahniidae, as Linyphiidae, for example, which do not seem to be influenced by mowing. Linyphiidae are on the contrary frequently and abundantly cited in studies on ballooning (e.g. Dean and Sterling, 1985; Greenstone et al. 1987; Blandenier and Fürst 1998).

The IndVal analysis showed that some rare species were bound to control areas, in both types of vegetation. All individuals of *Bathyphantes setiger*, a very rare European species, were found in control plots, and this species had a significant IndVal for the CC (*Cladietum*, control). *Pirata piraticus* was also a characteristic species of CC, as were immatures of *Pirata* sp., very likely belonging to the same species. These taxa prefer wet conditions provided by the thick litter layer of CC. The taxa Thomisidae was characteristic of CC, probably because these ambush spiders are favoured by the structure of these control areas. The Salticidae were characteristic of SC (*Schoenetum*, control), because individuals of this family often prefer warm and sunny locations. These conditions are provided in the SC by a thick layer of dry leaves that isolates from the fresh and wet conditions prevailing near the soil.

Few taxa were characteristic of mown vegetation. Among them, some are favoured by the greater quantity of light that reaches the soil in this treatment type, such as *Arctosa* sp. (probably *A. leopardus*) for the SM (*Schoenetum*, mown) and *Trochosa* sp. (probably mostly *T. spinipalpis*) for the CM (*Cladietum*, mown). That Linyphiidae were characteristic species of the CM in the transects is possibly due to a methodological bias: small species building small webs near the ground are more likely to be uncovered in transects if there is little litter.

If we examine our data from the point of view of species rarity, we see no negative effect of mowing on stenotopic rare wetland species, contrary to the results of Decler (1990) in reedmarsh. The positive effect on WO species resulted from the opening of fens, allowing more light to reach the soil because of litter removing. A decrease in the number of RO species could be observed in the mown plots. This is at first sight surprising, but can be explained by the disappearance of the litter through mowing. This litter, which is particularly well developed in CC, and to a lesser extent in SC, supports a dry and warm microhabitat (Villepoux and Darinot 2001), which allows thermophilous species, such as *Neoscona adianta* in our study, to inhabit the *Cladietum*. It divides the habitat into a shady, humid understory below the layer of dead leaves, and a dry and warm one above. These authors emphasised the importance of this layer of dry leaves and the significance of its destruction for the marked impoverishment and standardisation of the *Cladietum* spider fauna following mowing and grazing. However, even though we perceived a similar effect to what Villepoux and Darinot (2001) mentioned for the Lavours marshes (about 250 km south-west of our site, near the Rhone river), it was much less dramatic in our study, because our geographic situation is much less favourable for thermophilous species than the Rhone valley.

Decler (1990) showed an increase in ubiquitous species following mowing in reedmarsh. Our data did not show such an effect, with few individuals of ubiquitous species being caught (e.g. *Erigone dentipalpis*, *Bathyphantes gracilis*, *Araeoncus humilis*). However, our study took place in the second growing season after management, and it is thus possible that ubiquitous species were already excluded by more competitive wetland specialists.

The negative effect on some families and on some rare species shown in this study is particularly interesting, because it gives evidence for the fact that mowing produces demonstrable effects on spider communities even during the second season after management. Two main reasons can be invoked to explain the persistence of these modifications in the spider community. The first is the destruction by mowing of habitat structures indispensable for the establishment of specialised species linked to these structures. The second is the difficulty of some groups of species to recolonise an environment, because of reduced dispersal abilities.

5.4. Management suggestions

A positive effect of mowing on stenotopic wetland spider species, which would have been of greatest interest, was not perceivable. The only positive effects concerned species of open habitats. Since some rare species (*Bathyphantes setiger*, *Satlatlas britteni*, *Clubiona subtilis* and *Neon valentulus*) and less mobile families (Hahniidae and Clubionidae), were mostly found within the control vegetation, one must fear that management could eventually eliminate these

taxa. On the other hand, previous studies have shown that management is a necessity to ensure the durability of the Grande Cariçai marshes, because of brushwood encroachment and succession.

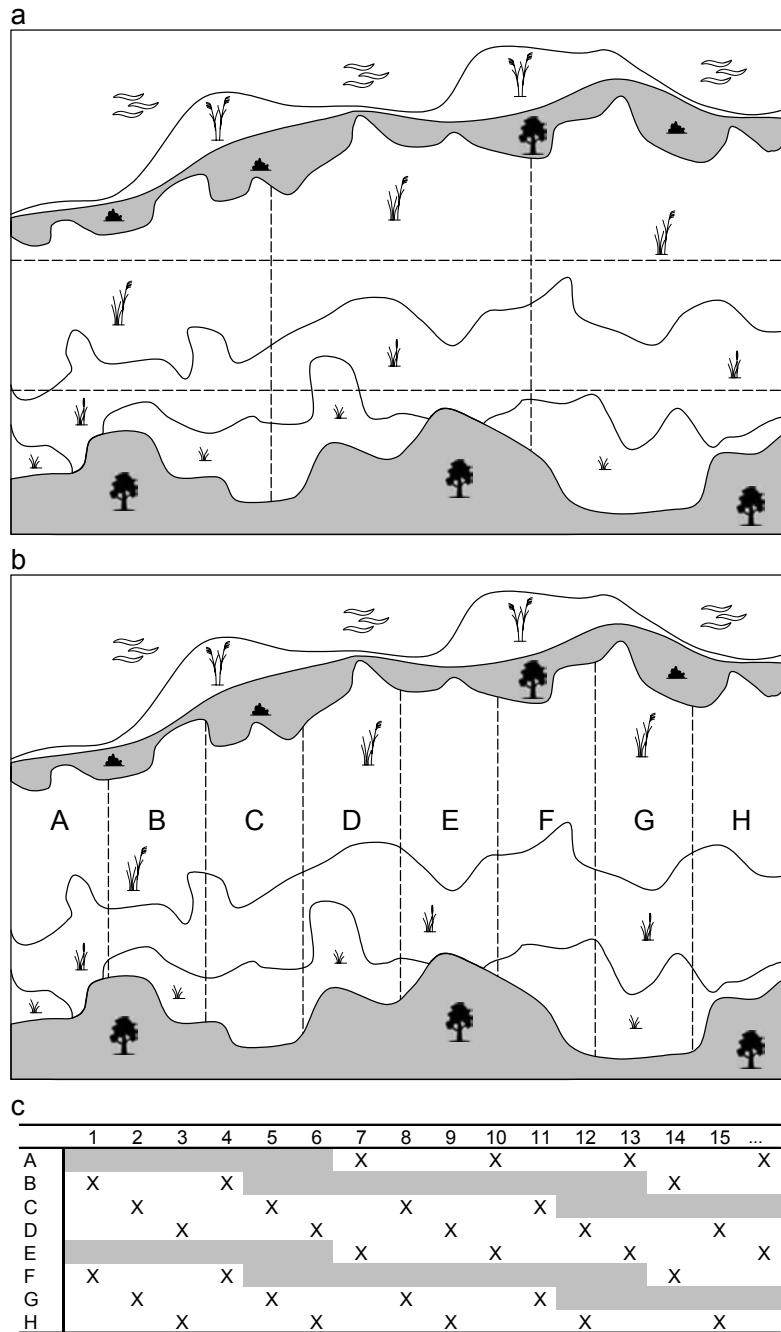


Fig. 3. Sketches of present (a) and proposed (b) management schemes for the mowing of the wet meadows in the Grande Cariçai. Mowing sectors are delimited by broken lines. They are mown triennially in (a), and following a three years and a ten years period in (b). Proposed mowing regime is given in (c), with A to H corresponding to sectors in (b), column header to years, and a X indicating that the sector is mown; grey shades show sectors unmanaged during 10 years.

Villepoux and Darinot (2001) emphasised the dissimilarity between the reactions of invertebrates and those of vegetation to management and consequently the necessity to study

them simultaneously. Many invertebrates, especially spiders, are sensitive to changes in vegetation structure, which is not easily taken into account in vegetation monitoring. These authors advocated carrying out a mosaic management, with refuge areas to which the fauna of mown plots can escape. Several authors (e.g. Decler 1990; Gerstmeier and Lang 1996; Pozzi et al. 1998) insisted on the need for a mosaic rotation of management types to keep the greatest possible diversity of habitats. Such a management scheme could however be harmful for species with a low dispersal ability if the time interval between two mowings is short.

The present management scheme for the mown areas of the Grande Cariçaie consists of a rotational mowing of large areas (2-4 ha) that coincide more or less with the longitudinal vegetation zonation parallel to the lakeshore (Fig. 3a). This is not favourable for spiders and probably invertebrates in general, since large areas of the same vegetation type are mown at the same time. We propose a different management scheme: parcels 50 to 150 m wide perpendicular to the vegetation zonation, and mown in two rotations of three years and 10 years, in agreement with Morris (1971) (Fig. 3b and 3c). This practice will end up in smaller surfaces of each vegetation type managed simultaneously, and provide zones unmanaged for 10 years serving as refuges for less mobile taxa. Long-term studies on spiders and other arthropods are needed to assess the efficiency of this management scheme.

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Appendix. Species list classified according to valuation categories.

Ubiquitous species (UB): *Agracina striata*, *Araeoncus humilis*, *Araneus diadematus*, *Bathyphantes gracilis*, *Erigone dentipalpis*, *Micrommata virescens*, *Pisaura mirabilis*, *Porrhomma microphthalmum*, *Theridion pictum*, *Zora spinimana*.

Wetlands and other habitats species (WO) : *Araneus sturmi*, *Argiope bruennichi*, *Evarcha arcuata*, *Hahnha pusilla*, *Larinioides cornutus*, *Mangora acalypha*, *Myrmarachne formicaria*, *Pardosa prativaga*, *Pirata latitans*, *Sitticus caricis*, *Tetragnatha extensa*, *Tetragnatha pinicola*, *Theridion impressum*, *Trochosa spinipalpis*, *Walckenaeria nudipalpis*.

Widespread wetland species (WW) : *Antistea elegans*, *Arctosa leopardus*, *Clubiona phragmitis*, *Clubiona stagnatilis*, *Dolomedes fimbriatus*, *Gnathonarium dentatum*, *Gongyliidiellum murcidum*, *Pirata piraticus*, *Pirata piscatorius*, *Silometopus elegans*.

Rare wetland species (RW) : *Clubiona juvenis*, *Clubiona subtilis*, *Marpissa radiata*, *Microlinyphia impigra*, *Neon valentulus*, *Pirata tenuitarsis*, *Robertus insignis*, *Satlatlas britteni*, *Tibellus maritimus*.

Rare other habitats species (RO) : *Anelosimus vittatus*, *Bathyphantes setiger*, *Neoscona adianta*, *Thanatus striatus*, *Trichopterna thorelli*.

Abstract.

Meadows are often managed by mowing to prevent succession and brushwood encroachment. This management practice is efficient to maintain plant diversity, but the effect on arthropod groups is less well known. We sampled spiders in the Grande Cariçaie (Switzerland), a site of nature conservation importance, in two types of wet meadows, an unmanaged site and one two-years old mown conditions. Numbers of individuals for the most abundant families, diversity measures, and indicator taxa were compared among vegetation and treatment types. The results indicate that the less mobile spiders and species linked to litter or dead reeds, including rare species, are reduced by mowing. Present management consists in triennial mowing of 2 to 4 ha non-contiguous sectors. We investigate the conflict between the need to mow the meadows to maintain them, and the negative effect of mowing on spider communities. We therefore propose a new management scheme aimed at maintain the vegetation while lessening its negative effects on spider communities by providing refuges.

III Conservation of wet meadows by mowing: a food web approach¹

Introduction

Wetlands are among the most rare and most rich environments. Undamaged wetlands inhabit one quarter of the endangered animal species. Since the 19th century, 90% of the fens disappeared in Switzerland, and between 1965 and 1990, their surface has been divided by two (OFS 2002). In developed countries, important drainages to increase agricultural surfaces have resulted in a dramatic loss of wetlands surfaces. In the Swiss Plateau, the lowering of the lakes level resulted in the drainage of vast wetlands areas, and also in the apparition of wet meadows, in particular on the south shore of Lake Neuchâtel. The future of these meadows of high value for nature conservation is however not guaranteed, because of the disappearance of the natural dynamic and the presence of a rapid succession leading to terrestrialization. To avoid this negative evolution, mowing is a widely used nature conservation technique. Studies have been carried out to assess the impact of mowing, most of them on vegetation (e.g. Rowell 1985, Cowie et al. 1992, Buttler 1992, Güsewell et al. 1998) and invertebrates, mostly insects and spiders, (e.g. Morris 1979a, 1979b, 1981a, 1981b, 1987, Decler 1990, Dithlogo et al. 1992, Gerstmeier & Lang 1996, Klieber et al. 1995). Studies on limited taxonomic groups provide only partial information on the impact of cutting on a community. They do not permit the acquisition of an overall picture of its effect on the entire community. This management practice obviously strongly affects vegetation, increasing floristic diversity and decreasing plant biomass (Cowie et al. 1992, Buttler 1992, Güsewell et al. 1998). The perturbation of the community generated by mowing also affects indirectly the animal community. Mowing with hay removal has additional strong indirect effects, since it induces drastic changes in the environment structure, because of litter disappearance and modifications in vegetation height and structure (e.g. Morris 1971, Buttler 1987). These considerations highlight the need for analyses that include all taxonomic groups and the necessity to assess the impact of management on the structural organisation of a community and on ecosystem functioning. A food web, which depicts trophic interactions between organisms, is a commonly accepted way of describing a community's structure. Although empirical studies providing detailed descriptions of aquatic (Baird & Ulanowicz 1989, Warren 1989, Hall & Raffaelli 1991, Martinez 1991, Havens 1992, Tavares-Cromar 1996) and terrestrial (Polis 1991, Goldwasser & Roughgarden 1993) food webs have been carried out, food web analyses have to our

¹ Manuscript in preparation (Cattin, Banašek-Richter and Bersier)

knowledge not yet been used as a conservation tool to assess the impact of management on a terrestrial community.

Mowing represents an important part of the management scheme applied in the wet meadows of the Grande Cariçaie, a site of international importance for nature conservation (Ramsar Convention), located on the south shore of Lake Neuchâtel (Switzerland). Studies of the effect of this management technique on vegetation (e.g. Buttler 1987, 1992, Gusewell et al. 1998, 2000), nesting birds (Antoniazza & Maillefer 2001) and spiders (Cattin et al. 2003) have already been carried out at this location. A global study including all trophic levels and dealing with the effects that mowing has on the structure of fens communities will enhance the comprehension of the impact of the conservation methods used in the Grande Cariçaie. We examine here the differences between mown and control areas for some standard food-web properties, for functional diversity and diversity measures and for biomass quantities and taxa number among different trophic levels. As these descriptors concern the community functioning, we will put in evidence in this study effects that would not be perceivable in classical studies that deal only with restricted taxonomic groups.

Methods

Study site

The marshes of the Grande Cariçaie are mown once every three years to prevent succession (see Buttler et al. 1985 for a detailed description of the Grande Cariçaie). Our study sites (central coordinates on the Swiss national grid: 565.500/198.950, see Fig. 1) include two vegetation types, according to the Braun-Blanquet phytosociological classification: the *Cladietum marisci* Allorge 1922 (hereafter, Cladietum) and the *Orchio-Schoenetum nigricantis* Oberd. 1975 (hereafter, Schoenetum) (Buttler & Gallandat 1990). The main goals of the management of these areas by mowing are to reduce the high competitive potential of *Cladium mariscus* in the first association and to preserve the floristic diversity in the second (Buttler 1987). A control area has however been kept unmanaged since at least winter 1991–1992 for monitoring purposes. The managed part of the study area was last mown in March 1999.

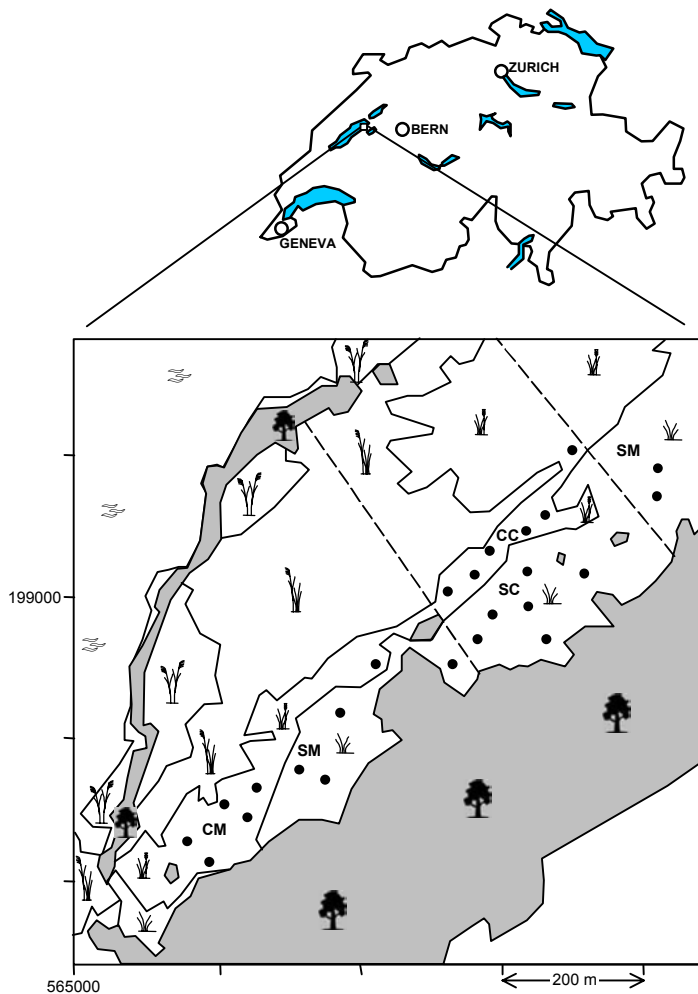


Fig. 1. Location of the study plots, in two vegetation types, mown triennially or unmanaged (control). CC: *Cladietum marisci*, control; CM: *Cladietum marisci*, mown; SC: *Orchio-Schoenetum nigricantis*, control; SM: *Orchio-Schoenetum nigricantis*, mown. Coordinates follow Swiss national grid. Dots indicate location of the cores. The control sector is delimited by broken lines.

Sampling

We randomly chose 24 plots at least 20 m apart, which were sampled during two periods, (1) from 24 May to 21 July and (2) from 21 August to 8 September 2000. A stratified sampling design was applied, with six plots sampled in each vegetation and treatment type: i.e. *Cladietum*-mown (CM), *Cladietum*-control (CC), *Schoenetum*-mown (SM) and *Schoenetum*-control (SC). Each plot was extensively sampled, with various techniques to ensure a precise and quantitative description of the species present above the ground and in the humus layer. An overall picture of the sampling methods applied in each station is given in Fig. 2. Litter, vegetation and small invertebrates living in the vegetation were sampled with cores measuring 0.5 m diameter ($\sim 0.2 \text{ m}^2$) and dug 0.2 m deep in the soil (see Fig. 3 for the material used for cores samples). These cores were taken early in the morning and hand-sorted a few hours later back to the laboratory, always by the same team, to ensure constant efficiency. The vegetation was cut and identified. Large arthropods and amphibians were also carefully collected along three transects 20 m long and of variable width: (1) 1 m wide, for large arthropods, mainly spiders, grasshoppers and crickets, (2) 1 m wide also, for amphibians and (3), 2 m wide, for Odonata. Small flying insects were collected with a 2 m X

2 m X 2 m tent made out from a mosquito net and dropped on the vegetation. Transects and tents were sampled at the middle of the day, to ensure arthropods to be active. For soil arthropods living in the humus layer, samples were taken using two cylinders 0.06 m in diameter ($\sim 0.01 \text{ m}^2$) and dug 0.1 m deep in the soil in each plot, once during the second sampling period. This approximation is possible because soil invertebrates densities, for example Acari, vary little between the beginning and the end of the summer (Block 1966). Arthropods were then extracted by means of a Berlese funnel. Invertebrates were then stored in 70% methanol. All methods were applied by favourable meteorological conditions. We chose sampling dates on windless and rainless days, with no rainfall during the preceding night. Plant species with very low densities were additionally sampled along three transects 50 m long and 1 m wide in each vegetation type. Identification was done when possible to the species level, sometimes requiring the help of specialized taxonomists, or to a coarser level for difficult groups (e.g. Acari, Chironomidae). Plant roots, bacteria and endoparasites were not sampled. "Species" and "taxon" are used interchangeably throughout this article.

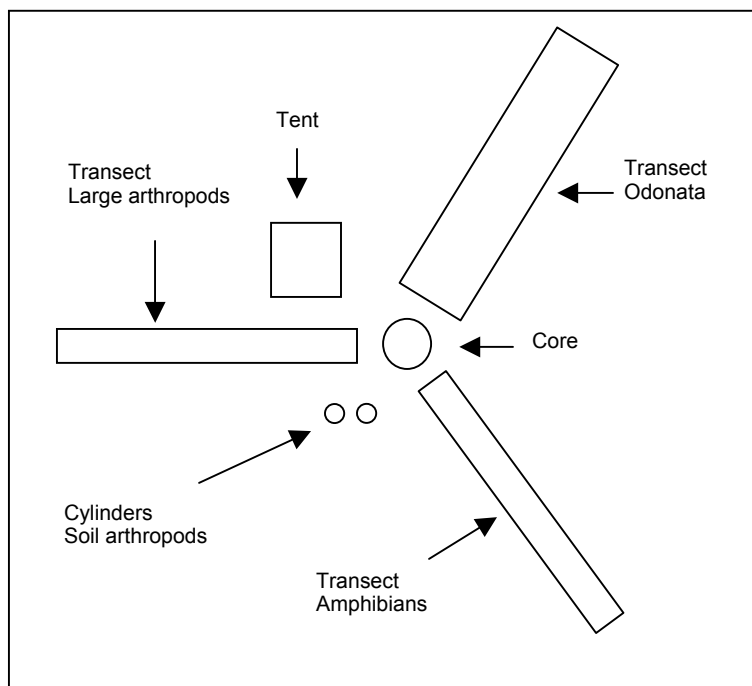


Fig. 2. Location of sampling methods applied in each station.

We pooled the data from the same vegetation type, treatment and sampling period to build eight food webs: Cladietum-control (CC1, CC2), Cladietum-mown (CM1, CM2), Schoenetum-control (SC1, SC2) and Schoenetum-mown (SM1, SM2). For each taxon, we kept the data obtained by the sampling method that provided the highest number of individuals per square meter to ensure the best sampling efficiency for the considered taxon.

Literature used for taxa identification can be found in Appendix 1.

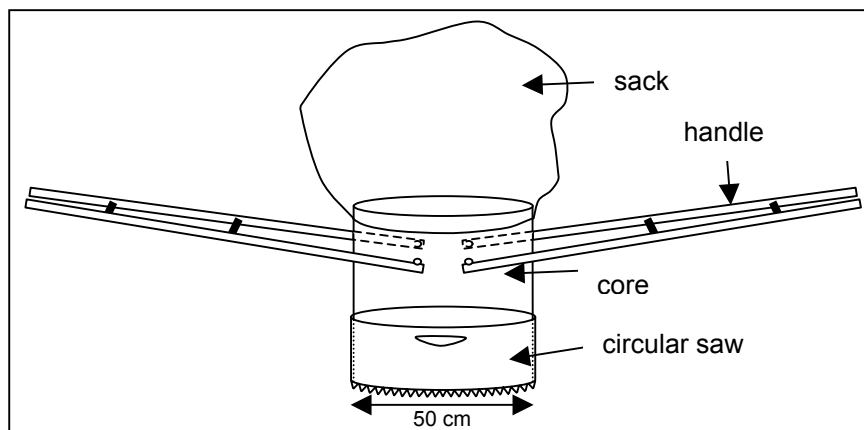


Fig. 3. Diagram of the sampling apparatus for cores.

Biomass estimation

Litter and vegetation from each 0.5 m diameter core were weighed in the dry state. Individuals (10 if possible) from plant species sampled along vegetation transects were also weighed in the dry state to determine a mean individual weight. Field and literature data were used to estimate vertebrates biomass. For invertebrates, excepted for very small taxa (e.g. Acari, Collembola), individuals of each taxon were measured and dry weighed to determine the linear relationship between log (length) and log (body mass). The length of all caught individuals was measured and their weight inferred by means of these relationships between log (length) and log (body mass). However, this method was not suitable for all taxa. There was no linear relationship between log (length) and log (body mass) in some groups, such as spiders of the family Lynphiidae, Heteroptera and some Diptera families. In other groups, we did not catch part of the individuals because of conservation reasons (frogs) or because of the technical difficulty of their capture (some spiders) or both (Odonata, Saltatoria and a few easily identifiable Coleoptera). In both conditions, individuals (4% of the total captures) were attributed the mean body mass of the taxon to which they belong or of the next higher taxon. The weight and length of Acari and Collembola, too small to be measured precisely, was attributed according to Macfadyen (1952).

Trophic relations

Trophic relations were mainly established from a thorough consultation of literature (Appendix 2) and internet sources, to which we added occasional field observations. As diet and behaviour can vary notably during the successive development stages of a species (e.g. litter feeding Diptera larvae and nectar feeding flying adults), we consider here immatures and adults belonging to the same taxon as different "species", i.e. we consider ontogenic species, following Schoenly and Cohen (1991). In taxonomic groups where several feeding

habits can be found (e.g. herbivores and predatory Acari), we divided the total biomass into equal parts. One major problem we encountered is the lack of precise data for the diet of many of the taxa sampled, especially for insects and spiders. Therefore, we used information about these taxa's size and behaviour to deduce their feeding habits. For example, a relatively large spider species building its web high in the vegetation (e.g. *Larinioides cornutus* (Clerck, 1757)) will not be able to catch a minute litter dwelling staphylinid beetle (e.g. *Anotylus intricatus* (Er.)) and is likely to prefer large flying insects like dragonflies (e.g. *Sympetrum sanguineum* (Müller)).

Food-web properties

Standard food-web properties were calculated for the eight webs. We determined the proportions of basal (without prey), intermediate (with both predators and prey) and top (without predators) species, B , I , and T , respectively. The ratio of predator to prey species P/P ($(T+I)/(I+B)$) was also calculated. TB , TI , II , and IB , the proportions of links between top and basal, top and intermediate, intermediate and intermediate, and intermediate and basal species, respectively, were determined. We computed link properties: L , the total number of links, DC , the directed connectance, which is the number of links divided by the squared number of species (S), LD , the linkage density (L/S). The mean maximum similarity of a web, $MxSim$, is the average of all species' largest value for trophic similarity. Trophic similarity between two species is measured as the number of prey and predators they share, divided by the pair's total number of prey and predators. The proportion of cannibalistic species, $Cannib$, was determined. As in previous studies describing species rich food webs with loops (e.g. Martinez 1991), we did not compute food chain length and other food chain properties because of computation time.

Trophic levels

To determine the biomass and the number of taxa in the different trophic levels for each food web, each taxon is attributed to a trophic level. Following Hairston and Hairston (1993), we consider only three trophic levels: basal species as the first level, herbivores and detritivores as the second level and a third level pooling carnivores and omnivores. These trophic levels are determined once in the matrix describing trophic links between all species, such that a given species belongs to the same trophic level in our eight food webs. This makes comparisons between food webs more sensible, as a species always has the same status. As mowing is practised with hay and litter removal, we separated litter from the biomass of the first trophic level, otherwise it would have resulted in the trivial result that biomass in the first trophic level decreases with mowing.

Diversity measures

Since all food webs were sampled with the same effort, a comparison between diversity indices is possible. As diversity indices are more meaningful if calculated on organisms belonging to a same ecological group, we computed them separately for each trophic level. In addition to the number of species S , we chose two indices, the reciprocal of Shannon diversity (the diversity number of Hill, 1973):

$$DN = e^H, \text{ with } H = -\sum_{i=1}^S p_i \cdot \ln p_i, \text{ where } p_i \text{ is the relative abundance of the } i\text{th species,}$$

and Pielou's evenness (Pielou 1966):

$$J = H / H_{\max} = \left(-\sum_{i=1}^S p_i \cdot \ln p_i \right) / \ln S.$$

We chose these indices despite their sensitivity to sampling effort (Gotelli & Graves 1996), because sampling effort is identical for the eight food webs. DN and J were computed on the densities of individuals (number of individuals/m²). All plant species having the same density, because individuals were not weighed separately (the concept of individual is difficult to define for plants growing in clumps), the interpretation of the two last indices for the first trophic level is difficult.

In addition to these classical diversity measures, we computed functional diversity, FD , (Petchey et al. 2002), which is defined as the total branch length of a functional dendrogram. We applied this measure to our eight food webs on the dendrogram of trophic similarity generated by a single linkage clustering (Legendre & Legendre 1998). The functional dendrogram is based here on the trophic similarity between species, transformed into distances. Computed in this way, FD gives a synthetic picture of the trophic structure of a food web. To make the comparison of the values of FD for our eight food webs possible, we divided the sum obtained by the addition of all branches of the dendrogram of trophic similarity by the number of species present in the web.

Statistical analyses

We used a sign test (Sokal & Rohlf 2000) to test for differences between food-web properties, biomass, number of taxa, diversity indices and functional diversity in each trophic level, in mown and control areas. As we have only two different types of meadows and two treatment types, 0.125 ($2 \cdot 1/2^4$) is the maximum level of significance that can be reached with this sampling design. Consequently, we will consider this result for a test as significant. This makes sense, as it means that all pairs of samples (e.g. SM1-SC1, SM2-SC2, CM1-CC1 and CM2-CC2) show an increasing or a decreasing tendency for the tested characteristic. No correction was applied for multiple testing.

We constructed yield-effort curves (Cohen et al. 1993) for the number of species sampled. We extrapolated to total species richness separately for plants and animals by fitting a Michaelis-Menton equation (Raaijmakers 1987) to the species accumulation curves (Colwell & Coddington 1994).

Results

We collected 8393 individuals belonging to 423 animal taxa. These taxa represent 33 orders and 147 families. Additionally to these taxa, 42 plant taxa were sampled. We constructed species accumulation curves (Colwell & Coddington 1994) separately for plant and animal species to check that the cumulative number of taxa reached an asymptote. We come close to such a plateau, with both taxonomic groups. We sampled respectively 86% and 74% of the expected number of species, which indicates an adequate sampling effort. The relatively low proportion of the expected animal species sampled is explained by the high number of taxa represented by only one individual, a common feature in invertebrates field studies, even with a high sampling effort. To ensure that our eight food webs can be considered as independent samples, we checked for the mean proportion of common taxa between pairs of samples from different treatments, vegetation types and sampling periods. When food webs from the same vegetation type and sampling period were compared between mown and control areas, 36% of the taxa were common to both treatments; for the same sampling period and treatment, between Schoenetum and Cladietum, 33% were common to both vegetation types; for the same vegetation and treatment, but between the first and the second period, 37% were common to both periods. Such a proportion of common species allows us to consider our eight food webs as independent samples. It gives also more weight to our results concerning food-web structure, as the conclusions are not based on data with too much redundancy between species lists.

The list of all taxa with their code, the species list for the eight food webs with their density of individuals (number of individuals/m²) and biomass density (g/m²), and the eight complete food web matrices can be found in Appendix 3.

Food-web properties

Variability between sampling periods was tested. We observed only very small differences for T (-0.001 - -0.019) and I (+0.004-0.051) but expected increases that were more important for S (+7 - +48) and L (+4 - +1084). The variation for both T and I was so small that it can be neglected. The increase in S and the concomitant increase in L are due to the progression of the number of taxa between early and late summer in an environment in which the vegetation growth, and the development of the species linked to it, is delayed

because of the elevated water level that maintains a colder environment. Differences between sampling periods will not be discussed further, as the sampling period has little effect on food-web parameters. The fact that an increase in S and L does not result in important modifications of the food-web properties is particularly interesting as it means that food-web structure in mown and control areas is robust and that the differences observed between mown and control meadows are really the consequence of differences in treatment.

Several food-web properties showed significant variation between mown and control areas (Table 1 and Fig. 4). Taxa were classified into the three conventional categories of basal, intermediate and top species. Basal “species” include plant material (vascular plants, algae and bryophytes), litter (decomposing organic material and a few fungi) and some invertebrates that do not feed in the adult stage, such as Ephemeroptera and some parasitic Hymenoptera. A significant increase in B with mowing was observed, even if it varied little (0.12-0.21). Intermediate species comprise mostly invertebrates and some vertebrates. Among these, some are considered as intermediate species only because we included links between haematophagous insects (Ceratopogonidae) and the roe deer (*Capreolus capreolus* L.), the fox (*Vulpes vulpes* L.), the grasshopper warbler (*Locustella naevia* (Boddaert)), the reed bunting (*Emberiza schoeniclu* (L.)), the smooth snake (*Coronella austriaca* Laurenti) and the ring snake (*Natrix natrix* (L.)). The proportion of intermediate species I showed little variation (0.78-0.87) but was significantly lower in managed areas. The only top species is the hobby (*Falco subbuteo* L.), because we considered it highly improbable that haematophagous insects would be able to feed on this bird. T was almost constant among food webs and varied only slightly from 0.01 to 0.03. P/P , the ratio of predator to prey species, varied a little more (0.79-0.89) and was significantly lower in mown areas.

food web	S*	T	I*	B*	P/P*	TB	TI	II*	IB*	DC	LD*	L*	MaxSim*	Cannib*
SC1	160	0.006	0.86	0.13	0.87	0	0.005	0.84	0.16	0.060	9.662	1546	0.73	0.075
SM1	168	0.006	0.78	0.21	0.79	0	0.004	0.71	0.29	0.071	11.90	1999	0.76	0.042
SC2	152	0.007	0.849	0.145	0.861	0	0.005	0.798	0.196	0.067	10.15	1542	0.74	0.07
SM2	161	0.025	0.78	0.20	0.82	0.002	0.051	0.64	0.30	0.071	11.51	1853	0.79	0.050
CC1	166	0.006	0.87	0.12	0.89	0	0.006	0.77	0.22	0.076	12.54	2082	0.78	0.060
CM1	202	0.005	0.83	0.17	0.84	0	0.002	0.73	0.26	0.072	14.53	2934	0.79	0.040
CC2	118	0.008	0.82	0.17	0.84	0	0.006	0.77	0.22	0.072	8.46	998	0.73	0.076
CM2	168	0.006	0.815	0.179	0.826	0	0.005	0.708	0.287	0.068	11.40	1915	0.76	0.05

Table 1. Food-web properties. A * indicates a significant difference between mown (M) and control (C) areas.

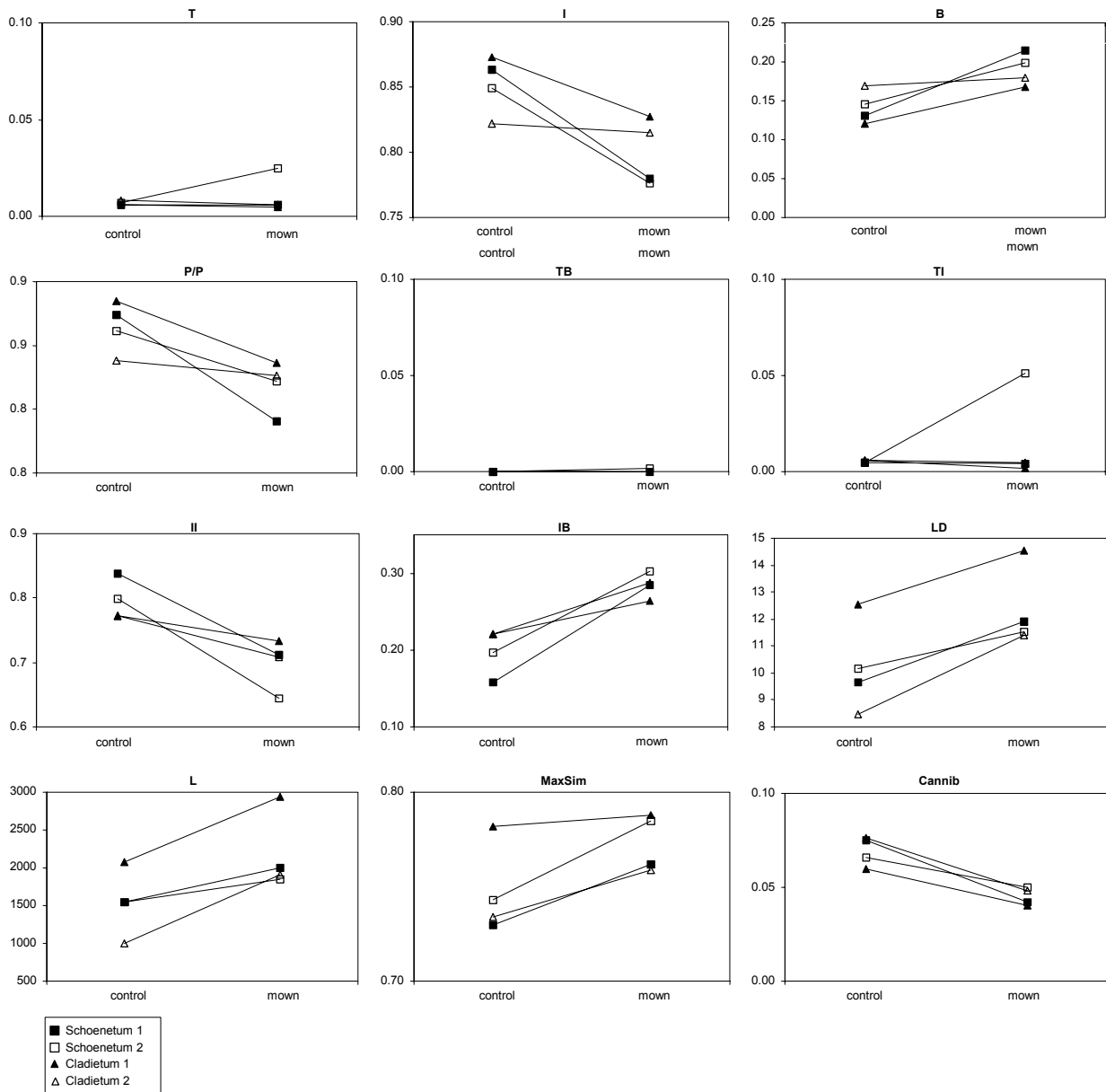


Fig. 4. Comparison of food-web properties between mown and control areas.

In line with this variation in the different species categories, link proportions also showed significant changes. The proportions of links involving intermediate species, *II* (0.64-0.84) and *IB* (0.16-0.30) varied the most. The proportion of links between intermediate species was lower in managed areas, while the proportion of links between intermediate and basal species increased with mowing. No significant change is observed for *TB* and *TI*, which vary as little as *T* (0-0.002 and 0.002-0.05, respectively). The linkage density (*LD*) differed greatly between food webs (8.46-14.53) and was significantly higher in mown areas. The total number of links (*L*), which ranges from 998 to 2934, followed the same trend. The maximum similarity (*MaxSim*) fluctuated little (0.73-0.79), but increased significantly with

management. The proportion of cannibalistic species (*Cannib*) showed the inverse trend, also with little variation (0.04-0.08).

Trophic levels

Litter quantity varied from 544 to 1477 g/m² and unsurprisingly decreased with mowing (Table 2 and Fig. 5). The reduction is however less important than expected, probably because the litter is not completely removed after mowing. The biomass (i.e. without litter) of the first trophic level (325–722 g/m²) was very large compared to the other levels. The biomass in the second trophic level ranged from 0.54 g/m² to 1.64 g/m² and in the third trophic level from 0.51 g/m² to 0.96 g/m². The total biomass in the first (without litter) and the third trophic levels significantly increased with mowing. The second level showed the opposite trend in managed areas. The respective proportions of biomass in the three defined trophic levels are in average 500/1.74/1.

food web	litter*	biomass 1*	biomass 2*	biomass 3*	nb taxa 1*	nb taxa 2	nb taxa 3*
SC1	758	363	1.081	0.516	21	56	83
SM1	544	563	1.042	0.538	32	53	83
SC2	784	325	0.896	0.513	22	58	72
SM2	626	535	0.537	0.955	32	53	76
CC1	1477	331	1.641	0.547	19	67	80
CM1	1265	722	1.128	0.746	32	70	100
CC2	1353	478	1.294	0.680	18	40	60
CM2	1285	587	0.916	0.799	29	60	79

Table 2. Biomass and number of taxa in each trophic level. A * indicates a significant difference between mown (M) and control (C) areas.

The number of taxa varied among trophic levels (Table 2 and Fig. 6). The first trophic level comprises 18 to 32 taxa, the second 40 to 70, and the third 60 to 100. Mowing resulted in an increase in the number of taxa in each trophic level, but this trend was only significant in the first and the third levels.

Diversity measures

The number of taxa (*S*) ranged from 118 to 202 (Table 3 and Fig. 7) among the eight individual food webs, for 466 sampled taxa. *S* was significantly greater in mown areas, an increase particularly striking in the Cladietum. The diversity number (*DN*) and the evenness index (*J*) show similar trends when a comparison is made between mown and control areas. *DN* in the first trophic level varied from 10.1 to 29.1 and significantly increased with mowing. *J* (range 0.80–0.99) in the same trophic level was also higher in managed Schoenetum, in the second period for Cladietum, but not in the first period for this last association. For the second trophic level, both *DN* (range 2.7–8.5) and *J* (range 0.25–0.54) decreased in mown areas, but this was only significant for the second index. In the third trophic level, both indices decrease with management; *DN* (range 2.6–6.6) and *J* (range 0.22–0.43) being significantly lower in mown meadows. *FD* varies from 0.28 to 0.36 and decreases with

management in all food webs, excepted in the first period for Cladietum, where it is almost constant.

food web	S*	DN 1 *	DN 2	DN 3 *	J 1	J 2 *	J 3	FD
SC1	160	13.07	8.46	3.91	0.84	0.53	0.31	0.35
SM1	168	29.14	2.70	2.65	0.98	0.25	0.22	0.33
SC2	152	16.40	8.17	3.65	0.92	0.52	0.30	0.33
SM2	161	29.14	3.15	2.63	0.98	0.29	0.22	0.32
CC1	166	18.60	8.31	6.55	0.99	0.50	0.43	0.28
CM1	202	29.12	7.91	5.10	0.98	0.49	0.35	0.29
CC2	118	10.07	7.29	5.45	0.80	0.54	0.41	0.36
CM2	168	24.32	7.35	4.04	0.96	0.49	0.32	0.33

Table 3. Diversity measures. A * indicates a significant difference between mown (M) and control (C) areas.

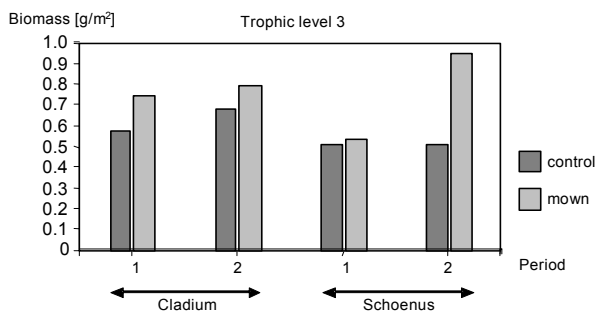
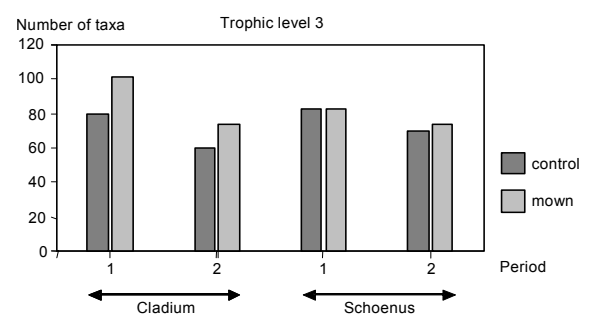
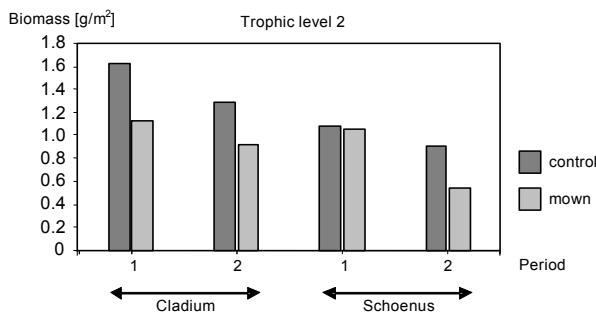
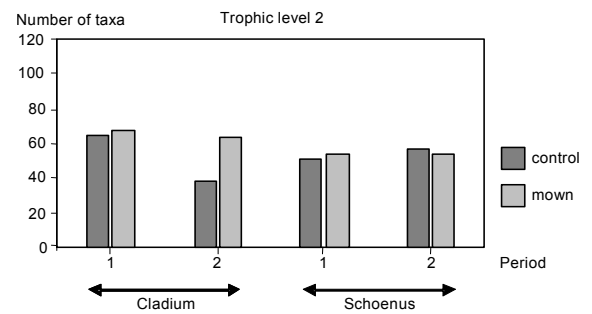
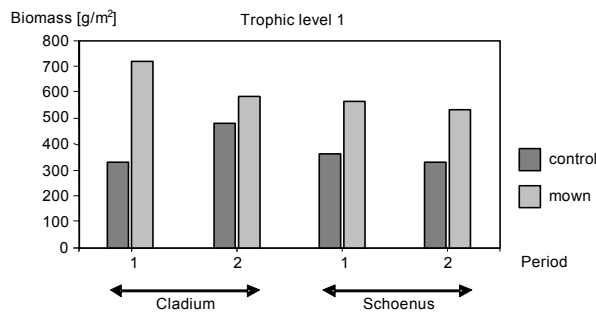
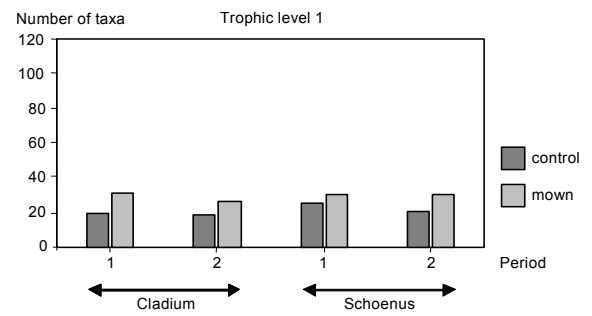
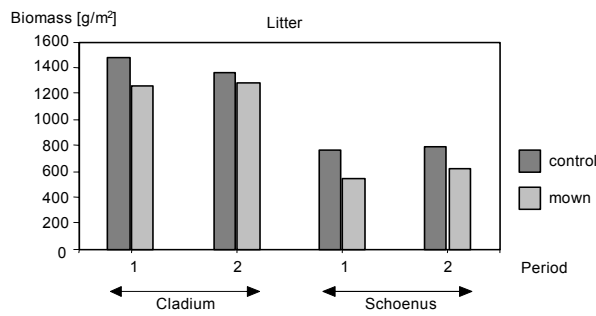


Fig. 5. Comparison of biomass quantities between mown and control areas.

Fig. 6. Comparison of the number of taxa between mown and control areas.

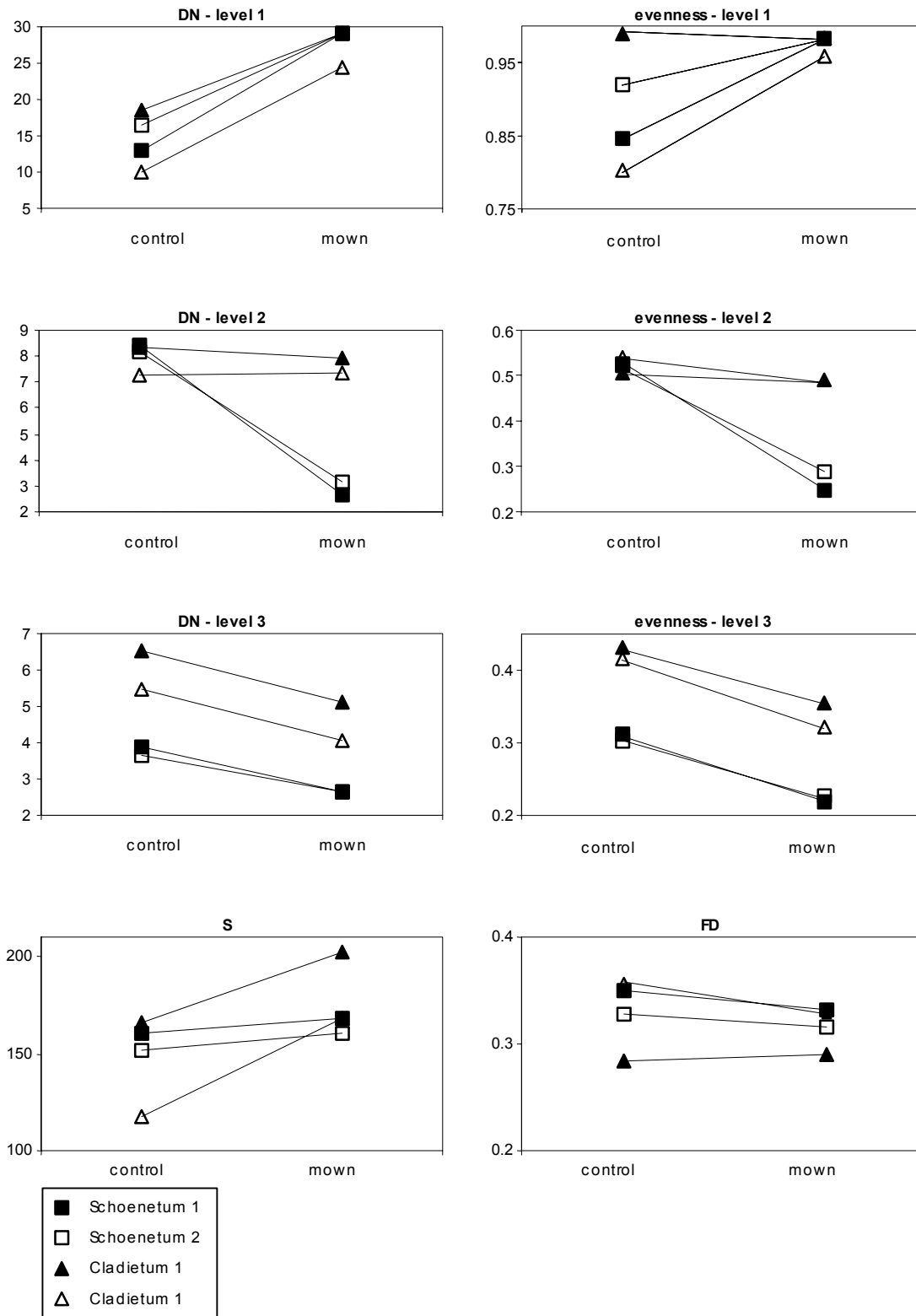


Fig. 7. Comparison of diversity measures between mown and control areas.

Discussion

The food-web approach to conservation applied here permitted us to reveal strong effects of mowing on the structure of food webs that would have been hidden with studies on

limited taxonomic groups. Our results highlight the influence that mowing has on the functioning of the community. The differences shown here between mown and control areas for food-web properties, biomass repartition among trophic levels and diversity measures can only be perceived with such global studies.

Food-web properties

The number of basal species increased with mowing. This is expected, as floristic diversity is known to benefit from mowing in the Grande Cariçaie, as has been put in evidence particularly in the Schoenetum (Buttler 1987). This variation in plant species number is the main factor that explains the variation in the number and the proportion of basal species. As there is no large change in T , the decrease in I associated with management results simply from the variation in B .

The different proportions of links vary little, apart from II and IB . The increase in IB with mowing is a consequence of the changes occurring among basal species. The dominant plant species in these marshes, such as *Schoenus* sp., *Cladium mariscus* (L.) and *Carex* sp. are not easily palatable. Only 4.6-8% of the net productivity of marsh and sedge grass is consumed against 14% of meadows plants (Pimentel 1975). The increase in the number of plant species in mown areas is made partly to the profit of more edible herbaceous plants (e.g. Poaceae). This fact supports the hypothesis that more herbivores inhabit managed meadows than control meadows. This is true in the Grande Cariçaie for the Schoenetum, where both the number and the proportion of herbivorous species (strict herbivores or omnivores that feed partly on plant items) increased with mowing, but not for the Cladietum. A more striking feature is the increase in the mean number of plant species eaten by each herbivore taxon, which varies between 4.9 and 7.4 in control areas and 10.7 and 21.3 in mown areas. This difference reflects the increase in the degree of generality of the herbivores inhabiting mown areas, revealed by the increase in IB . As both TB and TI are very low, because of the low number of top species in our food webs, II decreases in a comparable proportion as IB increases.

These results for herbivores foster the hypothesis that more generalist species should be found in mown areas for all trophic groups. We can imagine that in a stable, undisturbed food web, energy flows exploit specialized paths and that a perturbation of the community like mowing results in the loss of part of these paths. Specialized species are probably more sensitive to perturbations than generalists, and opportunistic species feeding on a wide range of prey could replace them. Indeed, L , the number of links in the food webs, is higher in mown areas, and more importantly, LD , which measures the linkage complexity, increases also with mowing. As the linkage density can be viewed as a measure of the degree of generality of the species composing a food web, mowing has possibly a negative effect on

the degree of specialization in a community. The increase in *MaxSim* can also be related to this hypothesis, as it indicates that species have a higher mean trophic similarity in mown areas. This supports the hypothesis that mown meadows are functionally less diverse than control meadows.

Trophic levels

The increase in the number of taxa for the first trophic level in managed areas is mostly explained by the increase in the number of plant species with mowing, as already shown by the increase in *B*. Biomass in trophic level 1 increases also for two abundant plant species: *Cladium mariscus* and *Campylium stellatum* (Schreb.). The increase in *Cladium mariscus* biomass (on average by 61%) is surprising, as one of the main goals of the management scheme in the Grande Cariçaie meadows is to control this potentially invading species. This astonishing result should question the efficiency of this management method in this meadow type. It should further be examined whether an effect on the vitality of this species (number of inflorescences) can be observed. The increase in the biomass of *Campylium stellatum* (136 %) is even greater, and can be explained by the fact that removing litter when the meadows are mowed leaves more space for mosses on the soil. The other plant species that significantly benefit from mowing are much less important in biomass (less than 5 g/m² in dry weight). Some are fully absent from control areas (*Mentha aquatica* L. and *M. arvensis* L.), whereas others are rare and show a great increase (90-200%) with mowing (*Galium palustre* L., *Hydrocotyle vulgaris* L., *Inula helvetica* G. Weber, *Lythrum salicaria* L., *Sanguisorba officinalis* L., *Fraxinus excelsior* L. and the family Poaceae). All these species also benefit from the higher light levels due to mowing with litter removal.

Biomass in trophic level 2 (i.e. herbivores and omnivores) decreased with mowing in the Cladietum and the Schoenetum. Among the taxa showing a biomass reduction, the larvae of the Diptera family Ceratopogonidae have the highest biomass density (0.21 g/m²). The strong decrease (-61%) for the larvae of this family can be explained by the fact that they probably greatly increase in mown areas during the first season after management, as they are an opportunistic family that profits from the strong perturbation of the meadows imposed by mowing, in particular because open mud appears. As our sampling takes place in the second year after management, we observe the decline of this taxon at the larval stage when the conditions are less favourable because vegetation cover closes again the openings due to mowing. The same ecological explanation can also be advanced to explain the decrease in biomass of the larvae of two other Diptera families, the Chironomidae and the Psychodidae. This hypothesis is corroborated by the fact that we found significantly more biomass of adults of the family Chironomidae in mown areas. The Collembola of the family Sminthuridae, although much less important in biomass, also decrease strongly in the mown

areas. This is probably explained by litter removal, as they are known to feed on decayed vegetation and microflora (Dindal, 1990). The last group decreasing with mowing is the larvae of the Homoptera family Delphacidae. Larvae are found in both sampling periods, and some species at least are known to overwinter as larvae (Morris 1981a); most of these larvae live in the litter. The litter removal could suppress both the individuals and the shelter where the Delphacidae spend the winter season. As larvae are wingless, they probably need time to recolonize areas out of which they have been eliminated.

Few taxa increase significantly in the third trophic level. Only the predatory Acari, immatures of the Lycosidae spider family *Arctosa* sp., and immatures of the spider family Salticidae increase significantly, but they represent only very small amounts of biomass.

Diversity measures

The variability in the number of species in the web is large, as the richest web has almost twice the number of species of the poorest (202 and 118). Compared to previously described terrestrial food webs (Polis 1991, Goldwasser & Roughgarden 1993), the number of species is high. The main reason for this high number of species is the relatively precise degree of taxonomic resolution reached here, especially for plant species and arthropods, even if not all taxa are identified to the species level.

An increase in the diversity number of Hill, DN , for the first trophic level is expected, given that plant species dominate this level in term of species number and of biomass, and that management in the Grande Cariçaie wet meadows has been shown to benefit floristic diversity (Buttler 1987). Our data show a strong increase in DN , obviously reflecting the strong increase in plant species number following mowing. The results for J would be more interesting if we had data on the number of individuals for plant species, instead of presence-absence data. The decrease in DN with mowing for the second and the third trophic levels has to be related to the decrease we observe for the number of intermediate species, because intermediate species can belong to both trophic levels, as herbivores as well as omnivores fall in the intermediate species category. This decrease is not significant for the second level, even though it is numerically very strong in the Schoenetum. Evenness in the second trophic level is also particularly strongly reduced by mowing in the Schoenetum. This decrease can probably be explained by the dominance of few species resulting from the perturbation of the community structure resulting from management. It is interesting to note that such a strong decrease in evenness is a particular feature of the second trophic level, highlighting the fact that the drastic changes in the litter and vegetation structure consecutive to management are especially affecting the community of herbivores and detritivores inhabiting these wet meadows. Changes in evenness for the third level are significant but much smaller. Two hypotheses can be proposed to explain this relatively modest decrease of

evenness in this last trophic level. Firstly, we know that most predators (e.g. spiders, dragonflies) are generalists. Changes in the repartition or in the kind of prey items upon which they feed (most of their prey belong to the second trophic level), have little influence on predators, even if these changes are large, as shown with the important variation in evenness observed in the second trophic level. Opportunistic feeders will only switch to the most abundant suitable prey taxa. Secondly, many predators are mobile species whose territories are larger than the size of a mown area (e.g. dragonflies, birds, lizards and snakes) or have good dispersal abilities (e.g. most spider species). Such species are not directly dependant on the changes in abundance and nature of the species of the second trophic level occurring in mown areas, because they can simply hunt elsewhere, where their typical prey are still present. Both hypotheses probably combine to explain the small influence that management has on the third trophic level. They also demonstrate the fact that our food web is probably a subsidized ecosystem, with part of the biomass imported from outside the boundaries of the different meadows types. Such allochthonous inputs probably particularly concern predator species. The difficulty in clearly determining food web boundaries is surely a general problem of food webs, especially of terrestrial ones (e.g. Cousins 1996, Polis & Hurd 1996).

Finally, functional diversity, *FD*, decreases slightly with mowing. This change reflects a reduction in trophic diversity, also shown by the increase in the food-web property *MaxSim* in mown meadows. This is likely to be induced by the simplification of the environment structure resulting from mowing, which leads to less diverse trophic niches and a higher trophic redundancy between species.

Our results demonstrate that mowing has different consequences depending on the trophic groups and levels in the Grande Cariçaie wet meadows. It clearly increased the total number of taxa, an increase particularly beneficial to species of the first trophic level. There is almost no impact on top species, and the impact on the third trophic level is hardly perceivable, because of the apparent dominance of generalist feeders in this level. The impact on intermediate species, and particularly on herbivores is much more interesting, as shown by the important changes in evenness in the second trophic level. If mowing results in a shift towards more generalist herbivores and detritivores to the detriment of specialized species, as our data indicates, it could be a particularly undesirable drawback of management in the Grande Cariçaie. Indeed, these marshes are the habitat of stenotopic species that cannot find similar environment elsewhere on the Swiss Plateau. If a change in the herbivore and the detritivore fauna towards more generalist species was confirmed by future studies over several consecutive years, it would point out a weakness of the conservation scheme.

Most studies on the effect of management in conservation concern the flora or predatory groups of invertebrates (spiders, Carabid beetles). There are two main postulates

behind these approaches. Firstly, invertebrate diversity is known to increase with plant structural diversity (Lawton 1983), a factor generally dependent on plant species diversity. Studies on the effect of management on the flora will then indirectly provide information on herbivore diversity and on the upper trophic levels. Secondly, studies on predatory groups are often chosen as indicative for general impacts of management on invertebrates, because they are supposed to integrate effects present on the lower trophic levels, and especially on herbivores. These approaches are appropriate to describe the impact of management on precise species or taxonomic groups, but cannot be used to assess its impact on a whole community. A food-web approach to the impact of conservation measures has precisely the advantage to provide information on the effect they have on the community functioning. A particularly interesting result of this study is the absence of differences in the structure of mown and control food webs between seasons, and the clear presence of such differences between food webs with different treatments, even if species composition varies strongly between sampling periods. This result indicates that the functioning of the community itself is affected by treatment, and that this functioning is stable throughout the studied seasons for the same treatment. It shows also that changes imposed by management in nature conservation sites are probably more complex and profound than those a species-based approach can reveal. Despite its complexity and despite the high taxonomic effort required, the food-web approach has the key advantage that it gives both a comprehensive view and an insight in the functional aspect of the implications of conservation techniques.

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Abstract.

Surface of wet meadows has decreased by 90% in Switzerland in the last century. They harbour a high number of endangered species. Presently, they are threatened by brushwood encroachment and terrestrialsation favoured by water regulation and draining. Mowing is a commonly used management technique to prevent this succession. Here, we analyse the effect of mowing in wet meadows of the Grande Cariçaie (Lake of Neuchâtel). Such studies typically tackle a single taxonomic group or some indicator species. We adopt a food-web approach whereby we focus on the structure and functioning of the community. Our results demonstrate that mowing has different consequences depending on the trophic groups and levels. It increased the total number of taxa, an increase particularly beneficial to species of the first trophic level. The impact on the third trophic level is hardly perceivable, because of the dominance of generalist feeders in this level. Intermediate species and particularly herbivores show the strongest change: mowing results in a shift towards more generalist herbivores and detritivores to the detriment of specialized species. It could be a particularly undesirable consequence of management, which is corroborated by a decrease in functional diversity in mown meadows.

Appendix 3.1 Species list

Identification of different taxonomic groups was performed by specialized taxonomists: H. Baur (part of Hymenoptera), G. Blandenier (Araneae), G. Carron (part of Saltatoria), J.-P. Haenni (Stratiomyidae, Scatopsidae), C. Liniger (Gastropoda), B. Merz (Sciomyzidae, Ulidiidae), L. Pollini (Dolichopodidae) and S. Whitebread (Lepidoptera).



illustration	code	taxon	family	order	class	kingdom
	28	Phragmites communis Trin.	Poaceae		Liliopsida	plantae
	8	Cladium mariscus (L.)	Cyperaceae		Liliopsida	plantae
	17	Galium palustre L.	Rubiaceae		Magnoliopsida	plantae
	36	Scutellaria galericulata L.	Lamiaceae		Magnoliopsida	plantae
	27	Peucedanum palustre (L.)	Apiaceae		Magnoliopsida	plantae
	18	Hydrocotyle vulgaris L.	Apiaceae		Magnoliopsida	plantae
	35	Schoenus nigricans L. + S. ferrugineus L.	Cyperaceae		Liliopsida	plantae
	26	Orchis palustris Jacq.	Orchidaceae		Liliopsida	plantae
	5	Carex hostiana (L.)	Cyperaceae		Liliopsida	plantae
	6	Carex sp.	Cyperaceae		Liliopsida	plantae
	39	Taraxacum palustre aggr.	Asteraceae		Magnoliopsida	plantae
	38	Spiranthes aestivalis (Poiret) Rich.	Orchidaceae		Liliopsida	plantae
	10	Epilobium palustre L.	Onagraceae		Magnoliopsida	plantae
	11	Epilobium sp.	Onagraceae		Magnoliopsida	plantae
	23	Lythrum salicaria L.	Lythraceae		Magnoliopsida	plantae
	22	Lysimachia vulgaris L.	Primulaceae		Magnoliopsida	plantae
	25	Molinia caerulea (L.)	Poaceae		Liliopsida	plantae
	24	Mentha aquatica L. + M. arvensis L.	Lamiaceae		Magnoliopsida	plantae
	40	Thalictrum flavum L.	Ranunculaceae		Magnoliopsida	plantae
	19	Inula helvetica G. Weber	Asteraceae		Magnoliopsida	plantae
7	Cirsium palustre (L.)	Asteraceae		Magnoliopsida	plantae	
12	Equisetum palustre L.	Equisetaceae		Equisetopsida	plantae	
34	Sanguisorba officinalis L.	Rosaceae		Magnoliopsida	plantae	
21	Linum catharticum L.	Linaceae		Magnoliopsida	plantae	
41	Utricularia sp.	Lentibulariaceae		Magnoliopsida	plantae	
15	Frangula alnus Miller	Rhamnaceae		Magnoliopsida	plantae	
16	Fraxinus excelsior L.	Oleaceae		Magnoliopsida	plantae	
2	Alnus glutinosa (L.)	Betulaceae		Magnoliopsida	plantae	
29	Pinus sylvestris L.	Pinaceae		Pinopsida	plantae	
32	Quercus robur L.	Fagaceae		Magnoliopsida	plantae	
33	Rhamnus catharticus L.	Rhamnaceae		Magnoliopsida	plantae	
13	Equisetum variegatum	Equisetaceae		Equisetopsida	plantae	
20	Juncus articulatus L.	Juncaceae		Liliopsida	plantae	
37	Solanum nigrum L.	Solanaceae		Magnoliopsida	plantae	
42	Veronica beccabunga L.	Scrophulariaceae		Magnoliopsida	plantae	
9	Calystegia sepium (L.)	Convolvulaceae		Magnoliopsida	plantae	
31	Poaceae	Poaceae		Liliopsida	plantae	
30	Plantae				plantae	
14	Fissidens sp.	Fissidentaceae		Bryopsida	plantae	
4	Campylium stellatum (Schreb.)	Amblystegiaceae		Bryopsida	plantae	
3	Bryopsida			Bryopsida	plantae	
1	algae				protista	
43	litter				detritus	
48	Hirudinea		Hirudinea	Annelida	animalia	
49	Glossiphonia heteroclita (L.)	Glossiphoniidae	Hirudinea	Annelida	animalia	
50	Haemopsis sanguisuga (L.)	Hirudinidae	Hirudinea	Annelida	animalia	
51	Oligochaeta		Oligochaeta	Annelida	animalia	
52	Oligochaeta larvae		Oligochaeta	Annelida	animalia	
53	Lumbricidae	Lumbricidae	Oligochaeta	Annelida	animalia	
54	Acari (predators)		Acari	Arachnida	animalia	
55	Acari (herbivores)		Acari	Arachnida	animalia	
56	Araneae		Araneae	Arachnida	animalia	



illustration	code	taxon	family	order	class	kingdom
	57	Agelenidae immature	Agelenidae	Araneae	Arachnida	animalia
	58	Araneidae immature	Araneidae	Araneae	Arachnida	animalia
	59	Araneus diadematus Clerck, 1757	Araneidae	Araneae	Arachnida	animalia
	60	Araneus sturmi (Hahn, 1831)	Araneidae	Araneae	Arachnida	animalia
	61	Argiope bruennichi (Scopoli, 1772)	Araneidae	Araneae	Arachnida	animalia
	62	Argiope bruennichi (Scopoli, 1772) immature	Araneidae	Araneae	Arachnida	animalia
	63	Larinioides cornutus (Clerck, 1757)	Araneidae	Araneae	Arachnida	animalia
	64	Larinioides sp. immature	Araneidae	Araneae	Arachnida	animalia
	65	Mangora acalypha (Walckenaer, 1802) immature	Araneidae	Araneae	Arachnida	animalia
	66	Neoscona adianta (Walckenaer, 1802)	Araneidae	Araneae	Arachnida	animalia
	67	Neoscona adianta (Walckenaer, 1802) immature	Araneidae	Araneae	Arachnida	animalia
	68	Clubiona juvenis Simon, 1878	Clubionidae	Araneae	Arachnida	animalia
	69	Clubiona phragmitis C. L. Koch, 1843	Clubionidae	Araneae	Arachnida	animalia
	70	Clubiona sp. immature	Clubionidae	Araneae	Arachnida	animalia
	71	Clubiona stagnatilis Kulczynski, 1897	Clubionidae	Araneae	Arachnida	animalia
	72	Clubiona subtilis L. Koch, 1867	Clubionidae	Araneae	Arachnida	animalia
	73	Gnaphosidae immature	Gnaphosidae	Araneae	Arachnida	animalia
	74	Zelotes sp. immature	Gnaphosidae	Araneae	Arachnida	animalia
	75	Antistea elegans (Blackwall, 1841)	Hahniidae	Araneae	Arachnida	animalia
	76	Antistea elegans (Blackwall, 1841) immature	Hahniidae	Araneae	Arachnida	animalia
	77	Hahnia pusilla C. L. Koch, 1841	Hahniidae	Araneae	Arachnida	animalia
	78	Hahnia sp. immature	Hahniidae	Araneae	Arachnida	animalia
	79	Hahniidae immature	Hahniidae	Araneae	Arachnida	animalia
	80	Micrommata virescens (Clerck, 1757) immature	Heteropodidae	Araneae	Arachnida	animalia
	81	Araeoncus humilis (Blackwall, 1841)	Linyphiidae	Araneae	Arachnida	animalia
	82	Bathypantes gracilis (Blackwall, 1841)	Linyphiidae	Araneae	Arachnida	animalia
	83	Bathypantes setiger F. O. P.-Cambridge, 1894	Linyphiidae	Araneae	Arachnida	animalia
	84	Erigone atra Blackwall, 1833	Linyphiidae	Araneae	Arachnida	animalia
	85	Erigone dentipalpis (Wider, 1834)	Linyphiidae	Araneae	Arachnida	animalia
	86	Gnathonarium dentatum (Wider, 1834)	Linyphiidae	Araneae	Arachnida	animalia
87	Gongyliidellum murcidum Simon, 1884	Linyphiidae	Araneae	Arachnida	animalia	
88	Lepthyphantes tenuis (Blackwall, 1852)	Linyphiidae	Araneae	Arachnida	animalia	
89	Linyphiidae immature	Linyphiidae	Araneae	Arachnida	animalia	
90	Meioneta rurestris (C. L. Koch, 1836)	Linyphiidae	Araneae	Arachnida	animalia	
91	Microlinyphia impigra (O. P.-Cambridge, 1871)	Linyphiidae	Araneae	Arachnida	animalia	
92	Porrhomma microphthalmum (O. P.-Cambridge, 1871)	Linyphiidae	Araneae	Arachnida	animalia	
93	Porrhomma oblitum (O. P.-Cambridge, 1871)	Linyphiidae	Araneae	Arachnida	animalia	
94	Satilatlas britteni (Jackson, 1912)	Linyphiidae	Araneae	Arachnida	animalia	
95	Silometopus elegans (O. P.-Cambridge, 1873)	Linyphiidae	Araneae	Arachnida	animalia	
96	Trichopterna thorelli (Westring, 1861)	Linyphiidae	Araneae	Arachnida	animalia	


illustration	code	taxon	family	order	class	kingdom
	97	Walckenaeria nudipalpis (Westring, 1851)	Linyphiidae	Araneae	Arachnida	animalia
	98	Agracina striata (Kulczynski, 1882)	Liocranidae	Araneae	Arachnida	animalia
	99	Liocranidae immature	Liocranidae	Araneae	Arachnida	animalia
	100	Arctosa leopardus (Sundevall, 1833)	Lycosidae	Araneae	Arachnida	animalia
	101	Arctosa leopardus (Sundevall, 1833) immature	Lycosidae	Araneae	Arachnida	animalia
	102	Arctosa sp. immature	Lycosidae	Araneae	Arachnida	animalia
	103	Lycosidae	Lycosidae	Araneae	Arachnida	animalia
	104	Lycosidae immature	Lycosidae	Araneae	Arachnida	animalia
	105	Pardosa prativaga (L. Koch, 1870)	Lycosidae	Araneae	Arachnida	animalia
	106	Pardosa sp.	Lycosidae	Araneae	Arachnida	animalia
	107	Pardosa sp. immature	Lycosidae	Araneae	Arachnida	animalia
	108	Pirata latitans (Blackwall, 1841)	Lycosidae	Araneae	Arachnida	animalia
	109	Pirata piraticus (Clerck, 1757)	Lycosidae	Araneae	Arachnida	animalia
	110	Pirata piscatorius (Clerck, 1757)	Lycosidae	Araneae	Arachnida	animalia
	111	Pirata sp. immature	Lycosidae	Araneae	Arachnida	animalia
	112	Pirata tenuitarsis Simon, 1876	Lycosidae	Araneae	Arachnida	animalia
	113	Trochosa sp. immature	Lycosidae	Araneae	Arachnida	animalia
	114	Trochosa spinipalpis (F. O. P.-Cambridge, 1895)	Lycosidae	Araneae	Arachnida	animalia
		115	Ero sp. immature	Mimetidae	Araneae	Arachnida
	116	Philodromidae	Philodromidae	Araneae	Arachnida	animalia
	117	Philodromidae immature	Philodromidae	Araneae	Arachnida	animalia
	118	Philodromus sp. immature	Philodromidae	Araneae	Arachnida	animalia
	119	Thanatus sp. immature	Philodromidae	Araneae	Arachnida	animalia
	120	Thanatus striatus C. L. Koch, 1845	Philodromidae	Araneae	Arachnida	animalia
	121	Tibellus maritimus (Menge, 1875)	Philodromidae	Araneae	Arachnida	animalia
	122	Tibellus sp.	Philodromidae	Araneae	Arachnida	animalia
	123	Tibellus sp. immature	Philodromidae	Araneae	Arachnida	animalia
	124	Dolomedes fimbriatus (Clerck, 1757)	Pisauridae	Araneae	Arachnida	animalia
	125	Dolomedes sp. immature	Pisauridae	Araneae	Arachnida	animalia
	126	Pisaura mirabilis (Clerck, 1757)	Pisauridae	Araneae	Arachnida	animalia
	127	Pisaura mirabilis (Clerck, 1757) immature	Pisauridae	Araneae	Arachnida	animalia
	128	Evarcha arcuata (Clerck, 1757)	Salticidae	Araneae	Arachnida	animalia
	129	Evarcha sp.	Salticidae	Araneae	Arachnida	animalia
	130	Evarcha sp. immature	Salticidae	Araneae	Arachnida	animalia
	131	Marpissa radiata (Grube, 1859)	Salticidae	Araneae	Arachnida	animalia
	132	Marpissa radiata (Grube, 1859) immature	Salticidae	Araneae	Arachnida	animalia
	133	Marpissa sp. immature	Salticidae	Araneae	Arachnida	animalia
	134	Myrmarachne formicaria (De Geer, 1778) immature	Salticidae	Araneae	Arachnida	animalia
	135	Neon valentulus Falconer, 1912	Salticidae	Araneae	Arachnida	animalia
	136	Salticidae	Salticidae	Araneae	Arachnida	animalia
	137	Salticidae immature	Salticidae	Araneae	Arachnida	animalia
	138	Sitticus caricis (Westring, 1861)	Salticidae	Araneae	Arachnida	animalia
	139	Sitticus sp. immature	Salticidae	Araneae	Arachnida	animalia
	140	Pachygnatha sp. immature	Tetragnathidae	Araneae	Arachnida	animalia
	141	Tetragnatha extensa (L., 1758)	Tetragnathidae	Araneae	Arachnida	animalia
	142	Tetragnatha pinicola L. Koch, 1870	Tetragnathidae	Araneae	Arachnida	animalia
	143	Tetragnatha sp.	Tetragnathidae	Araneae	Arachnida	animalia
	144	Tetragnatha sp. immature	Tetragnathidae	Araneae	Arachnida	animalia
	145	Tetragnathidae immature	Tetragnathidae	Araneae	Arachnida	animalia
	146	Anelosimus vittatus (C. L. Koch, 1836)	Theridiidae	Araneae	Arachnida	animalia




illustration	code	taxon	family	order	class	kingdom
	147	<i>Robertus insignis</i> O. P.- Cambridge, 1907	Theridiidae	Araneae	Arachnida	animalia
	148	<i>Robertus</i> sp. immature	Theridiidae	Araneae	Arachnida	animalia
	149	Theridiidae immature	Theridiidae	Araneae	Arachnida	animalia
	150	<i>Theridion impressum</i> L. Koch, 1881	Theridiidae	Araneae	Arachnida	animalia
	151	<i>Theridion pictum</i> (Walckenaer, 1802)	Theridiidae	Araneae	Arachnida	animalia
	152	<i>Theridion</i> sp. immature	Theridiidae	Araneae	Arachnida	animalia
	153	<i>Ozyptila</i> sp. immature	Thomisidae	Araneae	Arachnida	animalia
	154	Thomisidae immature	Thomisidae	Araneae	Arachnida	animalia
	155	<i>Xysticus</i> sp. immature	Thomisidae	Araneae	Arachnida	animalia
	156	<i>Zora</i> sp. immature	Zoridae	Araneae	Arachnida	animalia
	157	<i>Zora spinimana</i> (Sundevall, 1833)	Zoridae	Araneae	Arachnida	animalia
	158	Opilionida		Opilionida	Arachnida	animalia
	159	<i>Lithobius piceus</i> (L. Koch)	Lithobiidae	Lithobiida	Chilopoda	animalia
	160	<i>Lithobius</i> sp.	Lithobiidae	Lithobiida	Chilopoda	animalia
	161	<i>Lithobius</i> sp. larvae	Lithobiidae	Lithobiida	Chilopoda	animalia
	162	<i>Armadillidium opacum</i> (Brandt)	Armadillidiidae	Isopoda	Crustacea	animalia
	163	<i>Armadillidium pictum</i> (C. L. Koch)	Armadillidiidae	Isopoda	Crustacea	animalia
	164	<i>Armadillidium vulgare</i> (Latreille)	Armadillidiidae	Isopoda	Crustacea	animalia
	165	<i>Asellus aquaticus</i> (L.)	Asellidae	Isopoda	Crustacea	animalia
	166	<i>Ligidium hypnorum</i> (Cuvier)	Ligiidae	Isopoda	Crustacea	animalia
	167	<i>Ligidium hypnorum</i> (Cuvier) larvae	Ligiidae	Isopoda	Crustacea	animalia
	168	Porcellionidae immature	Porcellionidae	Isopoda	Crustacea	animalia
	169	<i>Porcellium conspersum</i> (C.L.Koch)	Porcellionidae	Isopoda	Crustacea	animalia
	170	<i>Trachelipus rathkei</i> (Brandt)	Trachelipidae	Isopoda	Crustacea	animalia
	171	Trichoniscidae	Trichoniscidae	Isopoda	Crustacea	animalia
	172	<i>Valvata</i> sp.	Valvatidae	Ectobranchia	Gastropoda	animalia
	173	<i>Lymnaea stagnalis</i> (L.)	Lymnaeidae	Hygrophila	Gastropoda	animalia
	174	<i>Stagnicola corvus</i> (Gmelin)	Lymnaeidae	Hygrophila	Gastropoda	animalia
	175	<i>Anisus leucostoma</i> (Millet)	Planorbidae	Hygrophila	Gastropoda	animalia
	176	<i>Planorbis planorbis</i> (L.)	Planorbidae	Hygrophila	Gastropoda	animalia
	177	<i>Cochlicopa nitens</i> (M. von Gallenstein)	Cochlicopidae	Stylommatophora	Gastropoda	animalia
	178	<i>Euconulus alderi</i> (Gray)	Euconulidae	Stylommatophora	Gastropoda	animalia
	179	<i>Zonitoides nitidus</i> (O. F. Müller)	Gastrodontidae	Stylommatophora	Gastropoda	animalia
	180	<i>Cepaea hortensis</i> (Müller)	Helicidae	Stylommatophora	Gastropoda	animalia
	181	Helicidae	Helicidae	Stylommatophora	Gastropoda	animalia
	182	<i>Trichia sericea</i> (Draparnaud)	Hygriiidae	Stylommatophora	Gastropoda	animalia
	183	Limacidae	Limacidae	Stylommatophora	Gastropoda	animalia
	184	<i>Oxyloma elegans</i> (Risso)	Succineidae	Stylommatophora	Gastropoda	animalia
	185	<i>Oxyloma elegans</i> (Risso) immature	Succineidae	Stylommatophora	Gastropoda	animalia
	186	<i>Succinea putris</i> (L.)	Succineidae	Stylommatophora	Gastropoda	animalia
	187	<i>Acanthinula aculeata</i> (O. F. Müller)	Valloniidae	Stylommatophora	Gastropoda	animalia
	188	<i>Vallonia costata</i> (O. F. Müller)	Valloniidae	Stylommatophora	Gastropoda	animalia
	189	<i>Vallonia pulchella</i> (O. F. Müller)	Valloniidae	Stylommatophora	Gastropoda	animalia
	190	<i>Vertigo antivertigo</i> (Draparnaud)	Vertiginidae	Stylommatophora	Gastropoda	animalia
	191	<i>Vertigo moulinsiana</i> (Dupuy)	Vertiginidae	Stylommatophora	Gastropoda	animalia
	192	<i>Vertigo pygmaea</i> (Draparnaud)	Vertiginidae	Stylommatophora	Gastropoda	animalia
	193	<i>Oxychilus cellarius</i> (O. F. Müller)	Zonitidae	Stylommatophora	Gastropoda	animalia
	194	Insecta larvae			Insecta	animalia
	195	Blattodea larvae		Blattodea	Insecta	animalia
	196	Pseudomopidae larvae	Pseudomopidae	Blattodea	Insecta	animalia
	197	Coleoptera larvae		Coleoptera	Insecta	animalia
	198	<i>Cytillus sericeus</i> (F.)	Byrrhidae	Coleoptera	Insecta	animalia
	199	<i>Pelochares versicolor</i> (Waltl)	Byrrhidae	Coleoptera	Insecta	animalia



illustration	code	taxon	family	order	class	kingdom
	200	<i>Cantharis fulvicollis</i> (F.)	Cantharidae	Coleoptera	Insecta	animalia
	201	<i>Cantharis rufa</i> (L.)	Cantharidae	Coleoptera	Insecta	animalia
	202	<i>Acupalpus flavicollis</i>	Carabidae	Coleoptera	Insecta	animalia
	203	<i>Agonum thoreyi</i> (Dejean)	Carabidae	Coleoptera	Insecta	animalia
	204	<i>Agonum viduum</i> (Panzer)	Carabidae	Coleoptera	Insecta	animalia
	205	Carabidae	Carabidae	Coleoptera	Insecta	animalia
	206	Carabidae larvae	Carabidae	Coleoptera	Insecta	animalia
	207	<i>Carabus granulatus</i> (L.)	Carabidae	Coleoptera	Insecta	animalia
	208	<i>Demetrias imperialis</i> (Germar)	Carabidae	Coleoptera	Insecta	animalia
	209	<i>Diplocampa assimile</i> (Gyllenhal)	Carabidae	Coleoptera	Insecta	animalia
	210	<i>Odacantha melanura</i> (L.)	Carabidae	Coleoptera	Insecta	animalia
	211	<i>Pterostichus minor</i> (Gyllenhal)	Carabidae	Coleoptera	Insecta	animalia
	212	<i>Pterostichus</i> sp.	Carabidae	Coleoptera	Insecta	animalia
	213	<i>Pterostichus strenuus</i> (Panzer)	Carabidae	Coleoptera	Insecta	animalia
	214	Cerambycidae larvae	Cerambycidae	Coleoptera	Insecta	animalia
	215	<i>Aphthona lutescens</i> (Gyll.)	Chrysomelidae	Coleoptera	Insecta	animalia
	216	<i>Chaetocnema confusa</i> (Bohem.)	Chrysomelidae	Coleoptera	Insecta	animalia
	217	Chrysomelidae	Chrysomelidae	Coleoptera	Insecta	animalia
	218	<i>Lema melanopus</i> (L.)	Chrysomelidae	Coleoptera	Insecta	animalia
	219	<i>Propylaea quatuordecimpunctata</i> (L.)	Coccinellidae	Coleoptera	Insecta	animalia
	220	<i>Chilocorus bipustulatus</i> (L.)	Coccinellidae	Coleoptera	Insecta	animalia
	221	<i>Limnobaris dolorosa</i> (Goeze, 1777)	Curculionidae	Coleoptera	Insecta	animalia
	222	<i>Dryops auriculatus</i> (Geoffr.)	Dryopidae	Coleoptera	Insecta	animalia
	223	<i>Dryops</i> sp.	Dryopidae	Coleoptera	Insecta	animalia
	224	<i>Bidessus unistriatus</i> (Schrank)	Dytiscidae	Coleoptera	Insecta	animalia
	225	<i>Colymbetes fusca</i> (L.)	Dytiscidae	Coleoptera	Insecta	animalia
	226	<i>Graptodytes granularis</i> (L.)	Dytiscidae	Coleoptera	Insecta	animalia
	227	<i>Polyhydrus lineatus</i> (F.)	Dytiscidae	Coleoptera	Insecta	animalia
	228	<i>Agriotes lineatus</i> (L.)	Elateridae	Coleoptera	Insecta	animalia
	229	<i>Agriotes</i> sp.	Elateridae	Coleoptera	Insecta	animalia
	230	Elateridae larvae	Elateridae	Coleoptera	Insecta	animalia
	231	<i>Anacaena limbata</i> (F.)	Hydrophilidae	Coleoptera	Insecta	animalia
	232	<i>Cercyon sternalis</i> (Sharp.)	Hydrophilidae	Coleoptera	Insecta	animalia
	233	<i>Chaetarthria seminulum</i> (Herbst)	Hydrophilidae	Coleoptera	Insecta	animalia
	234	<i>Enochrus testaceus</i> (F.)	Hydrophilidae	Coleoptera	Insecta	animalia
	235	<i>Anthocomus coccineus</i> (Schall.)	Malachiidae	Coleoptera	Insecta	animalia
	236	<i>Meligethes</i> sp.	Nitidulidae	Coleoptera	Insecta	animalia
	237	<i>Oedemera nobilis</i> (Scop.)	Oedemeridae	Coleoptera	Insecta	animalia
	238	<i>Brachygluta</i> sp.	Pselaphidae	Coleoptera	Insecta	animalia
	239	<i>Bryaxis bulbifer</i> (Reichb.)	Pselaphidae	Coleoptera	Insecta	animalia
	240	<i>Bryaxis</i> sp.	Pselaphidae	Coleoptera	Insecta	animalia
	241	<i>Euconnus hirticollis</i> (Illig.)	Scydmaenidae	Coleoptera	Insecta	animalia
	242	<i>Spanioconnus wetterhali</i> (Gyll.)	Scydmaenidae	Coleoptera	Insecta	animalia
	243	Aleocharinae	Staphylinidae	Coleoptera	Insecta	animalia
	244	<i>Anotylus intricatus</i> (Er.)	Staphylinidae	Coleoptera	Insecta	animalia
	245	<i>Anotylus</i> sp.	Staphylinidae	Coleoptera	Insecta	animalia
	246	<i>Cryptobium fracticorne</i> (Payk.)	Staphylinidae	Coleoptera	Insecta	animalia
	247	<i>Edaphus blühweissi</i> (Scheerp.)	Staphylinidae	Coleoptera	Insecta	animalia
	248	<i>Erichsonius cinerascens</i> (Grav.)	Staphylinidae	Coleoptera	Insecta	animalia
	249	<i>Euaesthetus ruficapillus</i> (Boisd.)	Staphylinidae	Coleoptera	Insecta	animalia
	250	<i>Gabrius femoralis</i> (Hochh.)	Staphylinidae	Coleoptera	Insecta	animalia
	251	<i>Hemistenus flavipes</i> (Steph.)	Staphylinidae	Coleoptera	Insecta	animalia
	252	<i>Hypocyphtus discoideus</i> (Er.)	Staphylinidae	Coleoptera	Insecta	animalia
	253	<i>Hypostenus latifrons</i> (Er.)	Staphylinidae	Coleoptera	Insecta	animalia
	254	<i>Hypostenus</i> sp.	Staphylinidae	Coleoptera	Insecta	animalia
	255	<i>Lathrobium fovalum</i> (Steph.)	Staphylinidae	Coleoptera	Insecta	animalia
	256	<i>Lesteva sicula</i> (Er.)	Staphylinidae	Coleoptera	Insecta	animalia
	257	<i>Myllaena dubia</i> (Grav.)	Staphylinidae	Coleoptera	Insecta	animalia
	258	<i>Myllaena minuta</i> (Grav.)	Staphylinidae	Coleoptera	Insecta	animalia






illustration	code	taxon	family	order	class	kingdom
	259	<i>Nestus carbonarius</i> (Gyll.)	Staphylinidae	Coleoptera	Insecta	animalia
	260	<i>Nestus mendicus</i> (Er.)	Staphylinidae	Coleoptera	Insecta	animalia
	261	<i>Nestus ruralis</i> (Er.)	Staphylinidae	Coleoptera	Insecta	animalia
	262	<i>Nestus</i> sp.	Staphylinidae	Coleoptera	Insecta	animalia
	263	<i>Oxytelus</i> sp.	Staphylinidae	Coleoptera	Insecta	animalia
	264	<i>Paederus riparius</i> (L.)	Staphylinidae	Coleoptera	Insecta	animalia
	265	<i>Parastenus</i> sp.	Staphylinidae	Coleoptera	Insecta	animalia
	266	<i>Platystethus nodifrons</i> (Sahlb.)	Staphylinidae	Coleoptera	Insecta	animalia
	267	<i>Platystethus</i> sp.	Staphylinidae	Coleoptera	Insecta	animalia
	268	Staphylinidae	Staphylinidae	Coleoptera	Insecta	animalia
	269	Staphylinidae larvae	Staphylinidae	Coleoptera	Insecta	animalia
	270	Staphylininae	Staphylinidae	Coleoptera	Insecta	animalia
	271	<i>Staphylinus erythropterus</i> (L.)	Staphylinidae	Coleoptera	Insecta	animalia
	272	<i>Stilicus rufipes</i> (Germ.)	Staphylinidae	Coleoptera	Insecta	animalia
	273	<i>Tetartopeus terminatum</i> (Grav.)	Staphylinidae	Coleoptera	Insecta	animalia
	274	<i>Trogophloeus corticinus</i> (Grav.)	Staphylinidae	Coleoptera	Insecta	animalia
	275	Entomobryomorpha		Collembola	Insecta	animalia
	276	Poduromorpha		Collembola	Insecta	animalia
	277	Sminthuridae	Sminthuridae	Collembola	Insecta	animalia
	278	Brachycera larvae		Diptera	Insecta	animalia
	279	Diptera		Diptera	Insecta	animalia
	280	Agromyzidae	Agromyzidae	Diptera	Insecta	animalia
	281	Athericidae	Athericidae	Diptera	Insecta	animalia
	282	Calliphoridae	Calliphoridae	Diptera	Insecta	animalia
	283	Cecidomyiidae	Cecidomyiidae	Diptera	Insecta	animalia
	284	Ceratopogonidae	Ceratopogonidae	Diptera	Insecta	animalia
	285	Ceratopogonidae larvae	Ceratopogonidae	Diptera	Insecta	animalia
	286	Chironomidae	Chironomidae	Diptera	Insecta	animalia
	287	Chironomidae larvae	Chironomidae	Diptera	Insecta	animalia
	288	Chloropidae	Chloropidae	Diptera	Insecta	animalia
	289	<i>Culex</i> sp.	Culicidae	Diptera	Insecta	animalia
	290	<i>Dixella</i> sp.	Dixidae	Diptera	Insecta	animalia
	291	<i>Argyra vestita</i> (Wiedemann, 1817)	Dolichopodidae	Diptera	Insecta	animalia
	292	<i>Campsicnemus scambus</i> (Fallén, 1823)	Dolichopodidae	Diptera	Insecta	animalia
	293	<i>Dolichopus nitidus</i> Fallén, 1823	Dolichopodidae	Diptera	Insecta	animalia
	294	<i>Dolichopus nubilius</i> Meigen, 1924	Dolichopodidae	Diptera	Insecta	animalia
	295	<i>Hercostomus assimilis</i> (Staeger, 1842)	Dolichopodidae	Diptera	Insecta	animalia
	296	<i>Teuchophorus calcaratus</i> (Macquart, 1827)	Dolichopodidae	Diptera	Insecta	animalia
	297	<i>Chrysotus cilipes</i> Meigen, 1824	Dolichopodidae	Diptera	Insecta	animalia
	298	Drosophilidae	Drosophilidae	Diptera	Insecta	animalia
299	Empididae	Empididae	Diptera	Insecta	animalia	
300	Ephydriidae	Ephydriidae	Diptera	Insecta	animalia	
301	Hybotidae	Hybotidae	Diptera	Insecta	animalia	
302	<i>Trigonometopus frontalis</i> (Meigen)	Lauxaniidae	Diptera	Insecta	animalia	
303	<i>Limonia</i> sp.	Limoniidae	Diptera	Insecta	animalia	
304	Limoniidae	Limoniidae	Diptera	Insecta	animalia	
305	Limoniidae larvae	Limoniidae	Diptera	Insecta	animalia	
306	Muscidae (nectarivores)	Muscidae	Diptera	Insecta	animalia	
307	Muscidae (coprophagous)	Muscidae	Diptera	Insecta	animalia	
308	Mycetophilidae	Mycetophilidae	Diptera	Insecta	animalia	
309	Phoridae	Phoridae	Diptera	Insecta	animalia	
310	<i>Pipinculus</i> sp.	Pipunculidae	Diptera	Insecta	animalia	
	311	Psychodidae	Psychodidae	Diptera	Insecta	animalia
	312	Psychodidae larvae	Psychodidae	Diptera	Insecta	animalia
	313	Rhagionidae larvae	Rhagionidae	Diptera	Insecta	animalia
	314	Rhinophoridae	Rhinophoridae	Diptera	Insecta	animalia




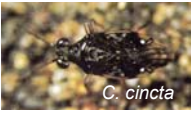
illustration	code	taxon	family	order	class	kingdom
	315	Sarcophagidae	Sarcophagidae	Diptera	Insecta	animalia
	316	Swammerdamella brevicornis (Meigen, 1830)	Scatopsidae	Diptera	Insecta	animalia
	317	Thripomorpha paludicola (Enderlein, 1905)	Scatopsidae	Diptera	Insecta	animalia
	318	Thripomorpha verralli (Edwards, 1934)	Scatopsidae	Diptera	Insecta	animalia
	319	Sciaridae	Sciaridae	Diptera	Insecta	animalia
	320	Ilione albiseta (Scopoli)	Sciomyzidae	Diptera	Insecta	animalia
	321	Ilione lineata (Fallén)	Sciomyzidae	Diptera	Insecta	animalia
	322	Limnia paludicola (Elberg)	Sciomyzidae	Diptera	Insecta	animalia
	323	Pherbellia schoenherri (Fallén)	Sciomyzidae	Diptera	Insecta	animalia
	324	Pherbina coryleti (Fallén)	Sciomyzidae	Diptera	Insecta	animalia
	325	Psacadina zernyi (Mayer)	Sciomyzidae	Diptera	Insecta	animalia
	326	Pteromicra leucopeza (?) (Meigen)	Sciomyzidae	Diptera	Insecta	animalia
	327	Sepedon spegea (Fabricius)	Sciomyzidae	Diptera	Insecta	animalia
	328	Sepedon spinipes (Scopoli)	Sciomyzidae	Diptera	Insecta	animalia
	329	Tetanocera ferruginea (Fallén)	Sciomyzidae	Diptera	Insecta	animalia
	330	Sphaerocidae	Sphaerocidae	Diptera	Insecta	animalia
	331	Nemotelus pantherinus (L., 1758)	Stratiomyidae	Diptera	Insecta	animalia
	332	Stratiomyidae larvae	Stratiomyidae	Diptera	Insecta	animalia
	333	Chrysotoxum sp.	Syrphidae	Diptera	Insecta	animalia
	334	Episyrphus balteatus (De Geer)	Syrphidae	Diptera	Insecta	animalia
	335	Neoascia sp.	Syrphidae	Diptera	Insecta	animalia
	336	Platycheirus sp.	Syrphidae	Diptera	Insecta	animalia
	337	Chrysops relictus (Meigen)	Tabanidae	Diptera	Insecta	animalia
	338	Haematopota sp.	Tabanidae	Diptera	Insecta	animalia
	339	Tabanus sp.	Tabanidae	Diptera	Insecta	animalia
	340	Tachinidae	Tachinidae	Diptera	Insecta	animalia
	341	Tipula sp.	Tipulidae	Diptera	Insecta	animalia
	342	Tipulidae	Tipulidae	Diptera	Insecta	animalia
	343	Tipulidae larvae	Tipulidae	Diptera	Insecta	animalia
	344	Herina frondescentiae (L.)	Ulidiidae	Diptera	Insecta	animalia
	345	Herina germinationis (Rossi)	Ulidiidae	Diptera	Insecta	animalia
	346	Herina parva (Loew)	Ulidiidae	Diptera	Insecta	animalia
	347	Otitinae	Ulidiidae	Diptera	Insecta	animalia
	348	Cloeon simile (Eaton)	Baetidae	Ephemeroptera	Insecta	animalia
	349	Procloeon bifidum (Bengtsson)	Baetidae	Ephemeroptera	Insecta	animalia
	350	Caenis sp.	Caenidae	Ephemeroptera	Insecta	animalia
	351	Heteroptera		Heteroptera	Insecta	animalia
	352	Heteroptera larvae		Heteroptera	Insecta	animalia
	353	Gerris sp.	Gerridae	Heteroptera	Insecta	animalia
	354	Hebridae larvae	Hebridae	Heteroptera	Insecta	animalia
	355	Hebrus pusillus (Fallen)	Hebridae	Heteroptera	Insecta	animalia
	356	Hebrus ruficeps (Thomson)	Hebridae	Heteroptera	Insecta	animalia
	357	Pachybrachius sp.	Lygaeidae	Heteroptera	Insecta	animalia
	358	Microphysidae	Microphysidae	Heteroptera	Insecta	animalia
	359	Stenodema calcaratum (Fallen)	Miridae	Heteroptera	Insecta	animalia
	360	Nabidae larvae	Nabidae	Heteroptera	Insecta	animalia
	361	Stalia boops (Schioedte)	Nabidae	Heteroptera	Insecta	animalia
	362	Pentatomidae larvae	Pentatomidae	Heteroptera	Insecta	animalia
	363	Sciocoris cursitans (Fall.)	Pentatomidae	Heteroptera	Insecta	animalia
	364	Sciocoris sp.	Pentatomidae	Heteroptera	Insecta	animalia
	365	Chartoscirta cincta (Herrich-Schäffer)	Saldidae	Heteroptera	Insecta	animalia
	366	Aphidina larvae		Homoptera	Insecta	animalia
	367	Aphidoidea		Homoptera	Insecta	animalia
	368	Aphidoidea larvae		Homoptera	Insecta	animalia
	369	Cicadina larvae		Homoptera	Insecta	animalia
	370	Cicadoidea		Homoptera	Insecta	animalia






illustration	code	taxon	family	order	class	kingdom
	371	Cicadoidea larvae		Homoptera	Insecta	animalia
	372	Fulgoroidea		Homoptera	Insecta	animalia
	373	Fulgoroidea larvae		Homoptera	Insecta	animalia
	374	Homoptera larvae		Homoptera	Insecta	animalia
	375	Sternorrhyncha larvae		Homoptera	Insecta	animalia
	376	Philaenus spumarius (L.)	Cercopidae	Homoptera	Insecta	animalia
	377	Deltocephalinae larvae	Cicadellidae	Homoptera	Insecta	animalia
	378	Typhlocybinae larvae	Cicadellidae	Homoptera	Insecta	animalia
	379	Delphacidae	Delphacidae	Homoptera	Insecta	animalia
	380	Delphacidae larvae	Delphacidae	Homoptera	Insecta	animalia
	381	Delphacinae larvae	Delphacidae	Homoptera	Insecta	animalia
	382	Cicadella viridis (L.)	Jassidae	Homoptera	Insecta	animalia
	383	Cicadella viridis (L.) larvae	Jassidae	Homoptera	Insecta	animalia
	384	Eupterygini	Jassidae	Homoptera	Insecta	animalia
	385	Jassidae	Jassidae	Homoptera	Insecta	animalia
	386	Jassidae larvae	Jassidae	Homoptera	Insecta	animalia
	387	Jassinae	Jassidae	Homoptera	Insecta	animalia
	388	Proctotrupeidea		Hymenoptera	Insecta	animalia
	389	Apis mellifera L.	Apidae	Hymenoptera	Insecta	animalia
	390	Hylaeus sp.	Apidae	Hymenoptera	Insecta	animalia
	391	Rhopalum sp.	Crabronidae	Hymenoptera	Insecta	animalia
	392	Diapriidae	Diapriidae	Hymenoptera	Insecta	animalia
	393	Eucoilidae	Eucoilidae	Hymenoptera	Insecta	animalia
	394	Aprostocetus sp.	Eulophidae	Hymenoptera	Insecta	animalia
	395	Ootetrastichus sp.	Eulophidae	Hymenoptera	Insecta	animalia
	396	Pediobius sp.	Eulophidae	Hymenoptera	Insecta	animalia
	397	Tetrastichus sp.	Eulophidae	Hymenoptera	Insecta	animalia
	398	Tetramesa sp.	Eurytomidae	Hymenoptera	Insecta	animalia
	399	Formica s.str. sp.	Formicidae	Hymenoptera	Insecta	animalia
	400	Formica sp.	Formicidae	Hymenoptera	Insecta	animalia
	401	Tetramorium sp.	Formicidae	Hymenoptera	Insecta	animalia
	402	Ichneumonidae	Ichneumonidae	Hymenoptera	Insecta	animalia
	403	Dipogon sp.	Pompilidae	Hymenoptera	Insecta	animalia
	404	Callitula ferrierei Boucek	Pteromalidae	Hymenoptera	Insecta	animalia
	405	Trypoxylon attenuatum (Smith)	Sphecidae	Hymenoptera	Insecta	animalia
	406	Trypoxylon clavicerum Lepeletier	Sphecidae	Hymenoptera	Insecta	animalia
	407	Blennocampinae	Tenthredinidae	Hymenoptera	Insecta	animalia
	408	Dolichovespula sylvestris (Scopoli)	Vespidae	Hymenoptera	Insecta	animalia
	409	Paravespula vulgaris (L.)	Vespidae	Hymenoptera	Insecta	animalia
	410	Lepidoptera		Lepidoptera	Insecta	animalia
	411	Lepidoptera larvae		Lepidoptera	Insecta	animalia
	412	Agrotis exclamationis (L.)	Noctuidae	Lepidoptera	Insecta	animalia
	413	Mythimna straminea (Treitschke)	Noctuidae	Lepidoptera	Insecta	animalia
	414	Anisoptera		Odonata	Insecta	animalia
	415	Zygoptera		Odonata	Insecta	animalia
	416	Aeschnidae	Aeschnidae	Odonata	Insecta	animalia
	417	Aeshna sp.	Aeschnidae	Odonata	Insecta	animalia
	418	Coenagrion pulchellum (Vander Linden)	Coenagrionidae	Odonata	Insecta	animalia
	419	Coenagrion sp.	Coenagrionidae	Odonata	Insecta	animalia
	420	Ischnura elegans (Vander Linden)	Coenagrionidae	Odonata	Insecta	animalia
	421	Somatochlora flavomaculata (Van der Linden)	Corduliidae	Odonata	Insecta	animalia
	422	Somatochlora sp.	Corduliidae	Odonata	Insecta	animalia
	423	Sympecma fusca (Vander Linden)	Lestidae	Odonata	Insecta	animalia
	424	Libellula depressa (L.)	Libellulidae	Odonata	Insecta	animalia
	425	Libellula quadrimaculata (L.)	Libellulidae	Odonata	Insecta	animalia
	426	Libellulidae	Libellulidae	Odonata	Insecta	animalia

illustration	code	taxon	family	order	class	kingdom
	427	<i>Orthetrum cancellatum</i> (L.)	Libellulidae	Odonata	Insecta	animalia
	428	<i>Orthetrum</i> sp.	Libellulidae	Odonata	Insecta	animalia
	429	<i>Sympetrum sanguineum</i> (Müller)	Libellulidae	Odonata	Insecta	animalia
	430	<i>Sympetrum</i> sp.	Libellulidae	Odonata	Insecta	animalia
	431	<i>Sympetrum striolatum</i> (Charpentier)	Libellulidae	Odonata	Insecta	animalia
	432	<i>Sympetrum vulgatum</i> (L.)	Libellulidae	Odonata	Insecta	animalia
	433	Chrysopidae larvae	Chrysopidae	Planipennia	Insecta	animalia
	434	Caelifera		Saltatoria	Insecta	animalia
	435	Ensifera		Saltatoria	Insecta	animalia
	436	Saltatoria		Saltatoria	Insecta	animalia
	437	Saltatoria larvae		Saltatoria	Insecta	animalia
	438	Acrididae	Acrididae	Saltatoria	Insecta	animalia
	439	Acrididae larvae	Acrididae	Saltatoria	Insecta	animalia
	440	<i>Chorthippus montanus</i> (Charpentier)	Acrididae	Saltatoria	Insecta	animalia
	441	<i>Chorthippus</i> sp.	Acrididae	Saltatoria	Insecta	animalia
	442	<i>Stethophyma grossum</i> (L.)	Acrididae	Saltatoria	Insecta	animalia
	443	<i>Pteronemobius heydenii</i> (Fischer, 1853)	Gryllidae	Saltatoria	Insecta	animalia
	444	<i>Tetrix</i> sp.	Tetrigidae	Saltatoria	Insecta	animalia
	445	<i>Tetrix subulata</i> (L.)	Tetrigidae	Saltatoria	Insecta	animalia
	446	<i>Conocephalus discolor</i> (Thunbg.)	Tettigoniidae	Saltatoria	Insecta	animalia
	447	<i>Conocephalus dorsalis</i> (Latr.)	Tettigoniidae	Saltatoria	Insecta	animalia
	448	Tettigoniidae larvae	Tettigoniidae	Saltatoria	Insecta	animalia
	449	Haplothrips sp.	Phlaeothripidae	Thysanoptera	Insecta	animalia
	450	Phlaeothripidae (predators)	Phlaeothripidae	Thysanoptera	Insecta	animalia
	451	Phlaeothripidae (herbivores)	Phlaeothripidae	Thysanoptera	Insecta	animalia
	452	<i>Limothrips denticornis</i> (Hal.)	Thripidae	Thysanoptera	Insecta	animalia
	453	Thripidae	Thripidae	Thysanoptera	Insecta	animalia
	454	Trichoptera larvae		Trichoptera	Insecta	animalia
	455	Leptoceridae	Leptoceridae	Trichoptera	Insecta	animalia
	456	Limnephiliidae	Limnephiliidae	Trichoptera	Insecta	animalia
	461	<i>Falco subbuteo</i> L.	Falconidae	Falconiformes	Aves	animalia
	462	<i>Locustella naevia</i> (Boddaert)	Sylviidae	Passeriformes	Aves	animalia
	463	<i>Emberiza schoeniclus</i> (L.)	Emberizidae	Passeriformes	Aves	animalia
	464	<i>Microtus agrestis</i> (L.)	Arvicolidae	Rodentia	Mammalia	animalia
	465	<i>Capreolus capreolus</i> L.	Cervidae	Artiodactyla	Mammalia	animalia
	466	<i>Vulpes vulpes</i> L.	Canidae	Carnivora	Mammalia	animalia
	44	<i>Hyla arborea arborea</i>	Hylidae	Anura	Amphibia	animalia
	45	<i>Rana</i> sp.	Ranidae	Anura	Amphibia	animalia
	46	<i>Rana temporaria temporaria</i>	Ranidae	Anura	Amphibia	animalia
	47	<i>Triturus</i> sp.	Salamandridae	Urodela	Amphibia	animalia
	457	<i>Lacerta agilis</i> L.	Lacertidae	Squamata	Reptilia	animalia
	458	<i>Anguis fragilis</i> L.	Anguidae	Squamata	Reptilia	animalia
	459	<i>Natrix natrix</i> (L.)	Colubridae	Squamata	Reptilia	animalia
	460	<i>Coronella austriaca</i> Laurenti	Colubridae	Squamata	Reptilia	animalia

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Appendix 3.2 Density of species [number of individuals / m²]

Presence/absence is given for all plant species; "code" refers to the species list; the eight food webs are designated by their code.

code	CC1	SC1	CM1	SM1	CC2	SC2	CM2	SM2
28	1	1	1	1	1	1	1	1
8	1	1	1	1	1	1	1	1
17	1	0	1	1	1	0	1	1
36	1	0	1	0	1	0	1	0
27	1	1	1	1	0	1	1	1
18	1	0	1	1	0	0	1	1
35	1	1	1	1	0	1	1	1
26	0	1	1	0	0	1	0	0
5	0	0	1	0	0	0	0	0
6	1	0	1	1	1	0	1	0
39	0	0	0	1	0	0	0	1
38	0	1	0	1	0	0	0	0
10	1	0	1	1	1	0	1	1
11	0	0	1	0	0	0	0	0
23	1	0	1	1	1	0	1	1
22	0	1	1	1	0	1	1	1
25	0	0	0	0	0	0	0	1
24	0	0	1	1	0	0	1	1
40	1	0	1	0	0	0	1	0
19	0	1	1	1	0	1	1	1
7	0	0	1	0	0	0	1	0
12	0	1	0	0	0	1	0	0
34	0	0	1	1	0	0	1	1
21	0	1	0	1	0	1	0	1
41	1	0	0	0	1	0	0	0
15	0	1	1	1	0	1	1	1
16	0	1	1	1	0	1	1	1
2	0	0	0	1	0	1	0	1
29	0	1	0	0	0	1	0	0
32	0	0	0	1	0	0	0	1
33	0	0	0	1	0	0	0	1
13	0	1	0	0	0	0	0	0
20	1	0	0	1	1	0	0	1
37	0	0	0	0	0	0	1	0
42	0	0	1	0	0	0	0	0
9	0	0	1	0	0	0	1	0
31	1	1	1	1	1	1	1	1
30	0	0	0	0	0	0	1	0
14	1	0	0	1	1	0	1	1
4	1	1	1	1	1	1	1	1
3	1	1	1	1	1	1	1	1
1	0	0	0	1	0	0	0	0
43	1	1	1	1	1	1	1	1
48	0	0	0	5.0968	0	0	0	0
49	0	0	0	0	5.0968	0	0	0
50	5.0968	0	5.0968	0	0	0	0	0
51	0	5.0968	0	8.4947	5.0968	5.0968	7.6453	15.583
52	0	0	0	5.0968	0	0	0	0

code	CC1	SC1	CM1	SM1	CC2	SC2	CM2	SM2
53	0	0	0	10.194	0	0	0	5.9684
54	597.35	1172.6	1161.5	2282.4	597.35	1172.6	1161.5	1982.5
55	597.35	1172.6	1161.5	2282.4	597.35	1172.6	1161.5	1982.5
56	0	0.05	0.075	0.05	0.05	0.05	0.05	0.15
57	5.0968	0	0	0	0	0	0	0
58	2.5734	0.45	1.7823	0.4	0.05	1.7323	5.0968	5.9684
59	0	0	0	0	0	0	0.05	5.9684
60	0	0.05	0	0	0	0	0	0
61	0	0	0	0	0	0.05	0	0.5
62	0	0	0.05	0	0	0	0	0
63	0	0.1333	0.1	0.25	0.05	0.05	0.075	0
64	2.1911	135.28	2.74	0.6625	0.4333	0.1833	0.6	1.2447
65	0	0	0	0	0.05	0.05	0.05	0
66	0.05	0.05	0.05	0.05	0	0	0	0
67	0.15	0.15	0.05	0	0	0	0	0
68	0	0	0	0	5.0968	0	0	0
69	0	0	0	0	0	0	0	5.9684
70	12.232	5.0968	6.1262	0.05	7.1356	9.1743	10.206	3.0342
71	5.0968	0	0	5.0968	0	0	0	0
72	0	0	0	0	0	10.194	0	0
73	0	0	0	0	0	0	0	10.632
74	0	0	5.0968	5.0968	0	5.0968	5.0968	5.9684
75	5.0968	0	5.0968	5.0968	6.1162	11.468	0	0
76	7.6453	13.592	7.6453	5.0968	10.194	6.8125	6.7958	5.9684
77	0	0	0	0	0	0	5.0968	0
78	0	0	0	0	5.0968	0	0	0
79	0	0	0	15.291	0	0	0	0
80	0	0	0	0	0	0.05	0	2.2395
81	0.25	0	0	5.0968	0	0	0	0
82	5.1968	0	5.0968	0	0	0	0	5.9684
83	11.893	5.0968	0	0	5.0968	0	0	0
84	0	0	0	0	0	0	0.25	0
85	0	0.05	0	5.0968	0	0	0	0
86	10.194	0	8.4947	0	5.0968	0	5.0968	0
87	5.0968	5.0968	24.21	7.6453	0	5.0968	5.0968	3.5811
88	0	0	0.25	0	0	0	0	0
89	94.801	25.534	37.377	30.581	50.119	43.323	62.861	47.119
90	0.25	0	0	0	0	0	0	0
91	0	0	0	0	0	0	0.05	0
92	0	5.0968	0	0	0	0	0	0
93	0	0.25	0	0	0	0	0	0
94	10.194	0	0	0	0	0	0	0
95	0	0	10.194	0	0	0	0	0
96	5.0968	0.05	0	0	0	0	0	0
97	0	0	5.0968	0	0	0	5.0968	0
98	0	0	0	5.0968	0	0	0	0
99	0	5.0968	10.194	0	0	0	5.0968	0
100	0	0	0	5.0968	0	0	0	0
101	0	0	0	112.13	0	0	0	0
102	0	0	7.6453	6.7958	5.0968	0	7.6453	7.8338
103	0.05	0.05	0.2	0.1	0.05	0	0	0
104	5.2218	5.0968	10.277	37.377	0	0	0	0
105	5.0968	0	2.5859	2.5859	0	0	0	0
106	0	0	0.05	0.1	0	0	0	0
107	0	0	0	0	12.232	15.291	9.1743	2.6261

code	CC1	SC1	CM1	SM1	CC2	SC2	CM2	SM2
108	0	0	0.05	0	0	0	0	0
109	6.7958	0	0	0.05	6.7958	0	5.0968	0
110	0	0	5.0968	0	0	0	0	0
111	64.22	10.194	15.291	9.3442	67.958	27.183	33.129	22.776
112	10.194	0	5.0968	5.0968	0	0	5.0968	0
113	0	0	5.0968	0	0	0	10.194	0
114	0	5.0968	0	0	0	0	0	5.9684
115	0	5.0968	0	0	0	0	0	0
116	0	0.05	0	0	0	0	0	0
117	7.6703	10.194	0	0	2.5734	5.0968	0.05	0
118	0.05	0	0	0	0	0	0	0
119	0	0	0	0	5.0968	0.05	5.0968	4.3769
120	0	0.05	0	0	0	0	0	0
121	0	0.05	0.05	0.05	0	0	0.05	0
122	0.0875	0	0	0.05	0.1	0.05	0	0.25
123	5.1135	5.0968	0.1333	1.7323	1.7489	3.4312	5.2093	4.0238
124	0.05	0	0	0.15	0	0.05	0	0
125	1.6	0.05	0.32	0.05	2.6734	0.34	0.1	0.1
126	0.1	0.05	0.05	0	0	0.05	0.1	0
127	0	0	0.05	0	5.0968	0	0	5.9684
128	0	0.1333	0	0.05	0	5.0968	0	0.375
129	0	0.05	0	0	0	0	0	0.5
130	0	0	0	0	0	2.5734	0.05	0.5
131	0.075	0	0.05	0.05	0	0.05	5.0968	0
132	0	0	1.2	0	0	0	0	0.5
133	0.1	0	0	0	0	0	0	3.2342
134	0	0	0	0	0	0	5.0968	0
135	0	5.0968	0	0	0	5.0968	0	0
136	0.05	0.125	0.05	0.175	0.05	0.05	0	3.2342
137	0	0.2375	5.0968	30.581	5.0968	8.932	10.194	5.9684
138	0	5.0968	0	5.0968	5.0968	0	0	0
139	0	0	0.1	0	0	0	0	5.9684
140	5.0968	0	5.0968	0	0	0	0	0
141	0	0.05	0.05	0	0	0.05	0	0
142	0.05	0	0	0	0	0	0	0
143	0	0	0.05	0.15	0	0	0	0
144	0.075	0.05	0.1	0.1167	0.05	0	0	3.2342
145	0.25	0	0.05	0	0	0	0	0
146	0	0.05	0	0	0	0	0	0
147	0	5.0968	0	0	0	0	5.0968	3.5811
148	0	0	0	0	0	5.0968	5.0968	0
149	0	10.194	0.05	0	5.0968	5.0968	0	0
150	0.05	0	0	0	0	0	0	0
151	10.194	0	0	0	0	0	0	0
152	0	0.05	5.0968	0	10.194	0	0.05	0
153	0	5.0968	0	0	0	10.194	0	1.1937
154	0.1	5.0968	7.6703	5.0968	5.0968	10.194	0	1.1937
155	0	0	5.0968	0	0	0	5.0968	0
156	0	5.0968	0	0	0	7.6453	5.0968	0
157	0	0	5.0968	0	0	0	0	0
158	0	0	0.05	0	0	0	0	0
159	0	0	0	0	0	0	5.0968	0
160	0	0	0	0	0	0	5.0968	0
161	0	0	0	0	0	0	5.0968	0
162	0	5.0968	0	0	0	0	0	0

code	CC1	SC1	CM1	SM1	CC2	SC2	CM2	SM2
163	0	5.0968	0	0	0	0	0	0
164	0	5.0968	5.0968	0	0	0	0	5.9684
165	0	0	0	0	5.0968	0	0	0
166	0	5.0968	0	0	0	10.194	0	5.9684
167	0	61.162	5.0968	0	0	5.0968	0	0
168	0	73.904	0	0	0	5.0968	0	0
169	0	0	0	0	0	10.194	0	5.9684
170	0	13.592	12.742	5.0968	10.194	11.893	5.0968	5.9684
171	0	35.678	5.0968	0	0	45.872	5.0968	0
172	0	0	5.0968	0	0	0	0	0
173	0	0	0	10.194	0	0	0	0
174	5.0968	0	0	5.0968	0	0	0	0
175	0	0	0	0	20.387	10.194	0	0
176	10.194	0	0	7.6453	0	0	0	0
177	0	0	0	0	0	0	5.0968	0
178	0	5.0968	5.0968	0	0	5.0968	0	1.1937
179	0	0	0	0	0	0	5.0968	0
180	0	5.0968	0	0	0	0	5.0968	0
181	5.0968	0	5.0968	0	0	0	5.0968	0
182	5.0968	0	5.0968	0	5.0968	5.0968	7.6453	0
183	0	5.0968	5.0968	0	0	0	0	0
184	11.213	5.0968	5.0968	5.0968	25.484	10.194	10.194	4.3769
185	5.0968	0	0	0	0	5.0968	0	0
186	5.0968	0	5.0968	0	0	5.0968	0	5.9684
187	0	0	0	0	0	10.194	0	0
188	0	0	0	0	0	0	5.0968	0
189	0	5.0968	0	0	0	0	0	5.9684
190	5.0968	0	5.0968	5.0968	0	7.6453	0	15.295
191	0	5.0968	5.0968	0	0	10.194	10.194	0
192	5.0968	5.0968	5.0968	0	0	0	0	0
193	5.0968	0	0	0	0	0	0	0
194	0	0	0	5.0968	0	0	0	0
195	0	5.0968	0	0	0	5.0968	0.05	0
196	0	0	0	0	0	5.0968	0	0
197	0	0	5.0968	5.0968	0	5.0968	10.194	5.9684
198	0	0	0	5.0968	0	0	0	0
199	0	0	0.25	0	0	0	0	0
200	0	0	0.25	0	0	0	0	0
201	0	0.05	0	0	0	0	0	0
202	0	5.0968	0	0	0	10.194	0	0
203	5.0968	0	0	0	0	0	0	0
204	5.0968	5.0968	10.194	0	0	0	5.0968	0
205	0	5.0968	0	0	0	0	0	0
206	5.0968	0	8.4947	5.0968	0	0	0	0
207	0	5.0968	0	0	0	0	0	0
208	0	0	0	0	0	0	5.0968	0
209	0	0	5.0968	0	0	0	0	0
210	0	0	0	0	10.194	0	0	0
211	0	0	0	0	0	0	0	5.9684
212	0	0	10.194	0	0	0	0	5.9684
213	0	7.6453	0	0	0	0	0	5.9684
214	0	0	0	5.0968	0	0	0	0
215	0	0	5.0968	0	0	0	0	0
216	0	0	0.25	5.0968	0	0	0	0
217	0	0	5.0968	0	0	0	0	0

code	CC1	SC1	CM1	SM1	CC2	SC2	CM2	SM2
218	0.25	0	0	0	0	0	0	0
219	0	0	0.25	0	0	0	0	0
220	0	0	0	0.25	0	0	0	0
221	0.0833	0	2.5984	0.075	0	0	5.0968	0
222	5.0968	12.742	7.6453	0	5.0968	5.0968	0	0
223	0	0	0	7.6453	0	5.0968	0	0
224	0	0	0	5.0968	5.0968	0	0	0
225	0	0	0	0	0.05	0	0	0
226	0	5.0968	0	0	0	0	0	0
227	0	0	0	0	5.0968	0	0	0
228	0	5.0968	0	5.0968	0	0	0	0
229	0.25	0	0	0	0	0	0	0
230	0	0	0	5.0968	0	5.0968	0	0
231	0	0	10.194	0	0	0	5.0968	0
232	0	0	0	0	5.0968	0	0	0
233	0	0	0	0	0	10.194	5.0968	5.9684
234	5.0968	0	0	0	0	0	0	0
235	0	0	0	0	0.05	0.25	0	0
236	0	0	2.375	0.25	0	0	0	0
237	0	0.25	0.05	0	0	0	0	0
238	0	0	5.0968	0	0	0	0	0
239	0	5.0968	0	0	0	0	0	0
240	0	5.0968	5.0968	5.0968	0	5.0968	0	0
241	0	0	0	0	0	0	7.6453	1.1937
242	0	0	0	0	0	0	0	5.9684
243	0	0	0	0	0	0	5.0968	5.9684
244	0	0.25	0	0	0	0	0	0
245	0	0	5.0968	0	0	0	0	0
246	0	0	0	5.0968	0	0	0	0
247	5.0968	5.0968	5.0968	0	0	5.0968	0	5.9684
248	0	0	5.0968	0	0	0	0	0
249	0	5.0968	0	0	0	5.0968	0	0
250	0	0	5.0968	0	0	0	0	0
251	0	0	0	0	0	0	5.0968	15.295
252	0	0	0	0	0	0	5.0968	0
253	5.0968	0	0	0	5.0968	0	0	0
254	5.0968	0	5.0968	0	0	0	0	0
255	0	0	5.0968	0	0	0	0	0
256	5.0968	0	5.0968	5.0968	0	5.0968	0	0
257	0	0	0	5.0968	0	0	0	4.3769
258	0	0	0	0	0	0	0	5.9684
259	5.0968	0	0	5.0968	0	5.0968	0	0
260	0	0	0	0	0	0	0	5.9684
261	0	0	0	5.0968	0	0	0	0
262	0	0	0	5.0968	0	0	0	0
263	0	0.25	0	0	0	0	0	0
264	0	5.1218	7.6453	1.7656	5.0968	5.0968	5.0968	0
265	0	0	0	0	0	0	5.0968	0
266	0	0	0.25	0	0	0	0	0
267	0.25	0	0	0.5	0	0	0	0
268	0	0	0	5.0968	0	0	0	5.9684
269	10.194	5.0968	10.194	10.194	5.0968	0	5.0968	0
270	0	5.0968	0	0	0	0	5.0968	0
271	0	0	0	0	0	0	0	5.9684
272	0	5.0968	5.0968	5.0968	5.0968	0	0	0

code	CC1	SC1	CM1	SM1	CC2	SC2	CM2	SM2
273	0	0	5.0968	0	0	0	0	0
274	0	0	5.0968	0	0	0	0	0
275	0	132.74	228.61	176.99	0	132.74	228.61	176.99
276	265.49	168.14	415.93	191.74	265.49	168.14	415.93	191.74
277	320.8	188.05	147.49	66.372	320.8	188.05	147.49	66.372
278	0	73.746	44.248	0	0	73.746	44.248	0
279	0	0.05	0	0	0	0	0	0
280	0	0	0	0	0	0	0	0.25
281	0	0.25	0	0	0	0	0	0
282	0.25	0.25	0.25	0	0.1833	0	0.25	0.25
283	3.6479	5.0968	0	0	0.25	0.375	0	1.1937
284	0.375	0.4375	0.9	0.31	0.25	0.3333	0.25	0
285	162.24	265.49	154.87	68.071	162.24	265.49	154.87	79.646
286	4.5323	3.6667	12.75	4.8078	4	3.4583	12.125	5.4167
287	77.434	44.248	44.248	0	77.434	22.149	32.896	0
288	0.25	0	0.375	0.05	0.7	5.7083	1.5	3.4375
289	0	0.25	0	0	0.3125	0.25	0.25	0
290	0	0	0	0	0	0	0	0.25
291	0	0	0.25	0	0	0	0	0
292	0	0	0	0	0	0	0.25	0
293	0	0	0	0	0	0	0.25	0
294	0.25	0	0.25	0	0	0	0	0
295	0	0	0.25	0	0	0	0	0
296	0	0	0.25	0	0	0	0	0
297	0	0	0.25	5.0968	0	0	0	0
298	0	0	0.25	0.25	0	0	0.25	0
299	0.25	0	0	0	0	0	0.25	0
300	0.25	0.25	0.25	0	0.25	0.25	0	0.25
301	0	0	5.0968	5.0968	1.5242	2.6734	1.8656	4.214
302	0	0	0	0	0	0	0.3333	0
303	0	0	0	0	0	0.25	0	0.25
304	0	0	2.6734	0	0.25	0.5	0.25	0
305	0	73.746	66.372	44.248	0	73.746	66.372	44.248
306	0.3542	0.125	0.4375	0.2083	0.3125	0.1563	0.1667	0.125
307	0.3542	0.125	0.4375	0.2083	0.3125	0.1563	0.1667	0.125
308	0	0	0	0	0	0	0.5	0
309	0.25	0	0	0	0	5.0968	0.3333	0
310	0	0	0.25	0	0	0	0.5	0.25
311	0	5.0968	5.0968	0	0	0	0.5	0
312	58.997	176.99	44.248	0	58.997	176.99	44.248	0
313	0	0	88.496	0	0	0	88.496	0
314	0.25	0	0	0	0	0	0	0
315	0.5	0	0	0.25	0	0	0	0
316	0.25	0.3333	0	0.25	0	0	0	0
317	0	0.25	0	0	0	0	0	0
318	0	0	0	0	0	0	0.25	0
319	3.4812	5.0968	0.2667	0.25	5.0968	0	1.8656	3.3592
320	0	0.25	0.3125	0	0	0.25	0	0.175
321	0	0	0.5	0	0	0	0.25	0.3333
322	0.5	1.0625	0.25	0.5	0	0	0	0
323	0	0	0	0	0	0	0.25	0
324	0.25	0	0.375	0	0	0	0	0
325	0	0	0	0	0	0.25	0.5	0
326	0	0	0	0	0.25	0	0	0
327	0	0	0	0	0.25	0	0	0

code	CC1	SC1	CM1	SM1	CC2	SC2	CM2	SM2
328	0.5	0	0	0.5	0.25	0	0	0.5
329	0	0	0.25	0	0	0	0	0
330	0.25	0	0	0	0	0	0	0
331	0.15	0	0	0	0	0	0	0
332	31.197	0	5.0968	0	44.248	0.05	0	0
333	0	0	0.25	0	0	0	0	0
334	0.25	0	0	0.25	0	0	0	0
335	0	0	0	0.25	0	0	0	0
336	0	0	0	0	0	0	0.25	0
337	0	0	0	0	0	0.5	0.05	0
338	0.05	0	0	0	0	0.25	0.25	0.5
339	0	0.25	0	0	0	0	0	0
340	0	0	0	0	0	0	0.25	0
341	0.25	0	0	0	0	0	0.25	0.5
342	0	0	0	0	0	0.25	0	0
343	0	0	44.248	0	0	0	44.248	0
344	0.5	0	0.75	1.125	0	0	0	0
345	0	0	0	0.5	0	0	0	0
346	0.25	0.625	0.25	1	5.0968	1.7117	0	0.25
347	0	0	0	0.05	0	0	0	0
348	0	0	0.5	0	0.25	0.25	0	0.3333
349	0	0	0	0	0	0	0	0.25
350	0	0	0	0	0.25	0	0	0
351	0	0	5.0968	0	0	0	0	0
352	15.291	0	22.936	8.4947	0	0	0	5.9684
353	0	0	0	0	5.0968	0	0	0
354	0	0	0	0	0	5.0968	0	0
355	0	0	7.6453	0	10.194	5.0968	0	13.339
356	0	0	0	0	0	5.0968	5.0968	0
357	5.0968	0	5.0968	0.25	6.1662	0	12.742	0
358	5.0968	0	0	0	0	0	0	0
359	0	0.25	0	0	0	0	0	0
360	2.5734	5.0968	0	0.05	0	0	0	0
361	0	0	0	0	0	5.0968	0	0
362	0.05	0	0.15	0	0	0	0	0
363	0	0	0	0	0	0	0	0.5
364	0	0	0	0.05	0	0	0	0
365	2.6734	0	5.0968	0.25	10.194	5.0968	0.25	0
366	0	0	0	0.75	0	0	0	0
367	0.05	2.7984	0.25	0.25	0	0	0	0
368	0.3333	0.5	0	0	0	0	0	0
369	7.6703	5.0968	7.6703	5.0968	0	30.581	0	2.3874
370	15.291	0	0	0	0	0	0	0
371	5.0968	0	0	0	1.25	4.5	0	0
372	10.194	0	0	0	0	0	0	0
373	0	0	5.0968	0	0	0	0	0
374	0	0	0	0	1.25	0	0	0
375	0.5	0	0	0	0	0	0	0
376	0	0	0	0	0	0.25	0	0.25
377	0.25	0	0	0	0	0	0	0
378	0	0	0	0	1	0	0	0
379	0	10.194	0	0	0	5.0968	0	0.25
380	48.93	12.805	27.183	2.7984	14.441	20.437	10.194	7.1712
381	0.25	0	0	0	0	0	0	0
382	0	0	0.75	0.375	0	0	0.5	0

code	CC1	SC1	CM1	SM1	CC2	SC2	CM2	SM2
383	0	0	0	0	0	0	0	0.25
384	0	0	0	0	0	0	15.313	16.25
385	0	0	0	0	0	0	0	0.5
386	5.0968	5.0968	0.25	0	1	2.95	5.25	9.9
387	0	0	0	0	5.0968	0	2.6734	0
388	0	15.291	5.0968	5.0968	0	7.6453	3.4812	3.2036
389	0	0	0.25	0	0	0	0	0
390	0	0.25	0	0	0	0	0.25	0
391	0.25	0	0	0	0	0	0	0
392	0	10.194	0	0	0	0	0	0
393	0	0	0	0	0	0.25	0	0
394	0	0	0	0.1	0	0	0	0
395	0	0	0	0	10.194	5.0968	5.0968	0
396	0	0	0	0	0	0	0	0.25
397	0	0	0.25	0	0	0	0	0
398	0	0	0.25	0	0	0	0	0
399	0	0.05	0	0	0	0	0	0
400	0	0	0	0	0	0.1	0	5.9684
401	0	0	5.0968	0	0	5.0968	0	1.1937
402	0.5	0.26	0.26	0.4167	0.375	0.375	0.75	0.25
403	0	0	0	0.25	0	0	0	0
404	0.05	0	0	0	0	0	0	0
405	0	0	0.25	0	0	0	0.25	0
406	0	0	0	0	0	0	0	0.25
407	0	0	0	0	0	0.2667	0	0
408	0	0	0	0	0	0.8	0	0
409	0	0	0	0	0.25	0	0	0
410	0.5	0	0.25	0.5	0.1833	0.25	0.375	0.5833
411	5.0968	0	0	0	5.0968	5.0968	0	4.7748
412	0	0.25	0	0	0	0	0	0
413	0.05	0	0	0	0	0	0	0
414	0.05	0.025	0.05	0.025	0	0.025	0.025	0.25
415	0.0375	0	0.025	0.025	0	0	0	0
416	0	0	0	0	0	0	0.025	0
417	0.025	0.025	0	0	0	0	0	0
418	0	0.5	0.25	0	0	0	0	0
419	0.025	0.0625	0.025	0.025	0	0	0	0
420	0	0.075	0	0.25	0	0	0	0
421	0	0.075	0.125	0.075	0	0	0	0.5
422	0.0417	0.025	0.075	0.0375	0.025	0.025	0	0.25
423	0	0	0	0	0	0	0	0.25
424	0.025	0	0	0	0	0	0	0
425	0	0.025	0	0.025	0	0	0	0
426	0.025	0	0	0	0	0	0	0
427	0	0	0	0	0	0.025	0	0
428	0	0	0	0	0	0	0.025	0
429	0.25	0	0	0	0.025	0.0813	0.0375	0.2833
430	0.0375	0	0.025	0.05	0.125	0.0667	0.0563	0.3375
431	0	0	0	0	0.0417	0.075	0.025	0
432	0.25	0	0	0.025	0.05	0.125	0.05	0.25
433	0.05	0	0.05	0	0	0	0	0
434	0	0	0	0	0	0.05	0.5	0.1
435	0	0	0	0.05	0	0	0	0
436	0.05	0	0	0	0	0	0	0.5
437	0	0	0	5.0968	0	0	0	0

code	CC1	SC1	CM1	SM1	CC2	SC2	CM2	SM2
438	0	0	0	0	0	0	0	0.75
439	0	0.05	0.25	0.3333	0	0	0	0.5
440	0	0	0	0	0	0.075	0	0.275
441	0	0	0	0	0	0	0	0.25
442	0.25	0	0	0	0	0	0.1	0
443	0	0	0.15	0	0	0	0	0
444	0	5.0968	0	0	0	0.05	5.0968	5.9684
445	0	0	0	0	0	2.5734	0	0
446	0	0	0	0	0	0	0	0.5
447	0.25	0	0.25	0	0	0	0.05	0.5
448	0	0	0.25	0.25	0	0	0	0
449	0.275	0	0	0	0	0	0	2.7853
450	0.125	0	0	0	1.2742	0	0	0
451	0.125	0	0	0	1.2742	0	0	0
452	0	0	0	0	0	0	0	5.9684
453	0.05	0	0	0	0	0	0	0
454	0	0	5.0968	0	0	0	5.0968	0
455	0.25	0	0	0.25	0	0	0	0
456	0	5.0968	0	0.05	0	0	0	0
461	1E-06	1E-06	1E-06	1E-06	1E-06	1E-06	1E-06	1E-06
462	0	4E-05	0	3E-05	0	4E-05	0	3E-05
463	5E-05	0	6E-05	0	5E-05	0	6E-05	0
464	0.0002	0.0004	0.0002	0.0004	0.0002	0.0004	0.0002	0.0004
465	1E-06	1E-06	1E-06	1E-06	1E-06	1E-06	1E-06	1E-06
466	1E-06	1E-06	1E-06	1E-06	1E-06	1E-06	1E-06	1E-06
44	0	0	0	0	0	0	0.05	0
45	0	0	0	0.05	0.05	0	0	0
46	0	0	0	0	0	0	0.075	0
47	0	0	0	0	0	0	0.05	0
457	0	0.0002	0	7E-05	0	0.0002	0	7E-05
458	0	0.0002	0	0.0001	0	0.0002	0	0.0001
459	6E-05	6E-05	6E-05	6E-05	6E-05	6E-05	6E-05	6E-05
460	0	0	0	7E-05	0	0	0	7E-05

Appendix 3.3 Biomass density of species [g / m²]

"code" refers to the species list; the eight food webs are designated by their code.

code	CC1	SC1	CM1	SM1	CC2	SC2	CM2	SM2
28	29.681	18.677	13.492	19.335	41.021	43.251	17.727	12.816
8	270.3	23.106	561.82	140.42	351.18	9.3272	421	104.09
17	0.0107	0	0.0258	0.4747	0.0107	0	0.2718	0.8982
36	0.0011	0	0.0043	0	0.0011	0	0.0043	0
27	0.0031	0.0061	0.0153	0.0031	0	0.0061	0.0153	0.0031
18	0.6116	0	1.0805	0.446	0	0	0.5861	0.3058
35	1.0364	199.35	0.1019	154.27	0	248.81	51.06	157.56
26	0	0.002	0.9174	0	0	0.002	0	0
5	0	0	12.436	0	0	0	0	0
6	16.463	0	15.838	11.774	22.082	0	11.995	0
39	0	0	0	0.0004	0	0	0	0.0005
38	0	0.0512	0	1.0364	0	0	0	0
10	0.0071	0	0.0193	0.0071	0.029	0	0.0193	0.0071

code	CC1	SC1	CM1	SM1	CC2	SC2	CM2	SM2
11	0	0	0.3568	0	0	0	0	0
23	0.0071	0	0.8318	0.5327	0.0071	0	0.1855	0.2948
22	0	0.1922	2.1138	0.032	0	0.1922	2.1138	0.032
25	0	0	0	0	0	0	0	42.686
24	0	0	0.0624	0.0327	0	0	0.2039	0.0327
40	1.4271	0	0.0016	0	0	0	0.0016	0
19	0	0.0218	1.4606	0.0872	0	0.0218	1.4606	0.0872
7	0	0	0.4201	0	0	0	0.4201	0
12	0	0.4587	0	0	0	1.2232	0	0
34	0	0	0.0669	0.1339	0	0	0.0669	0.1339
21	0	0.0007	0	0.0019	0	0.0007	0	0.0019
41	0.0559	0	0	0	0.1834	0	0	0
15	0	1.0237	1.4826	0.9178	0	1.0237	4.2813	0.9178
16	0	0.0151	0.0022	0.0605	0	0.033	0.0022	0.0605
2	0	0	0	0.0083	0	0	0	0.0083
29	0	0.0336	0	0	0	0.0336	0	0
32	0	0	0	0.0604	0	0	0	0.0604
33	0	0	0	0.0868	0	0	0	0.0868
13	0	2.1662	0	0	0	0	0	0
20	0.0124	0	0	0.0041	0.0124	0	0	0.0041
37	0	0	0	0	0	0	0.4077	0
42	0	0	0.2039	0	0	0	0	0
9	0	0	0.0107	0	0	0	0.0107	0
31	3.4659	0.9685	3.6697	4.7273	3.6442	0.0512	6.6004	16.14
30	0	0	0	0	0	0	0.2294	0
14	1.2742	0	0	21.126	0.0005	0	11.111	0.2039
4	2.2596	58.175	83.295	148.59	6.7873	20.77	43.298	191.53
3	4.4852	58.461	22.528	17.329	53.007	0.7136	14.271	6.9827
1	0	0	0	41.922	0	0	0	0
43	1477.2	757.98	1264.9	543.99	1353.1	784.15	1284.6	626.38
48	0	0	0	44.852	0	0	0	0
49	0	0	0	0	179.92	0	0	0
50	161.06	0	27.013	0	0	0	0	0
51	0	3.273	0	20.783	4.3323	4.0911	30.326	17.214
52	0	0	0	1.0194	0	0	0	0
53	0	0	0	9.3939	0	0	0	10.194
54	5.9735	11.726	11.615	22.824	5.9735	11.726	11.615	22.824
55	5.9735	11.726	11.615	22.824	5.9735	11.726	11.615	22.824
56	0	0.1577	0.2366	0.1577	0.1577	0.1577	0.1577	0.4731
57	2.5484	0	0	0	0	0	0	0
58	0.0301	0.0926	0.0579	0.0643	0.0005	0.0436	0.051	0.2548
59	0	0	0	0	0	0	1.11	30.071
60	0	0.055	0	0	0	0	0	0
61	0	0	0	0	0	2.1133	0	1.4075
62	0	0	0.0328	0	0	0	0	0
63	0	4.6067	4.7162	8.9023	0.5338	1.4831	1.4719	0
64	4.2142	3.8383	4.882	0.678	1.4123	0.578	1.9967	4.2904
65	0	0	0	0	0.005	0.005	0.0025	0
66	0.2665	0.245	0.4735	0.7121	0	0	0	0
67	0.785	0.04	0.315	0	0	0	0	0
68	0	0	0	0	3.0438	0	0	0
69	0	0	0	0	0	0	0	40.492
70	1.4076	0.139	6.1225	0.0022	1.9827	2.3616	8.2125	0.1287
71	36.188	0	0	24.595	0	0	0	0
72	0	0	0	0	0	2.3121	0	0

code	CC1	SC1	CM1	SM1	CC2	SC2	CM2	SM2
73	0	0	0	0	0	0	0	17.578
74	0	0	3.5678	2.5484	0	47.773	1.5291	13.761
75	3.6043	0	1.9453	1.9545	3.0904	6.2436	0	0
76	1.8757	3.0675	1.5992	2.6941	1.0232	1.3763	0.9817	0.5822
77	0	0	0	0	0	0	0.2548	0
78	0	0	0	0	0.051	0	0	0
79	0	0	0	2.7436	0	0	0	0
80	0	0	0	0	0	0.67	0	3.4847
81	0.0125	0	0	1.0194	0	0	0	0
82	1.1693	0	1.1468	0	0	0	0	1.2742
83	2.6758	1.1468	0	0	1.1468	0	0	0
84	0	0	0	0	0	0	0.075	0
85	0	0.0112	0	1.1468	0	0	0	0
86	4.5872	0	2.3998	0	1.1043	0	1.2954	0
87	0.7645	0.7645	2.6758	1.5291	0	0.5097	0.4247	0.5097
88	0	0	0.0562	0	0	0	0	0
89	16.965	4.5695	6.6888	5.4726	8.1955	9.5412	9.0584	10.236
90	0.0125	0	0	0	0	0	0	0
91	0	0	0	0	0	0	0.0112	0
92	0	1.1468	0	0	0	0	0	0
93	0	0.0562	0	0	0	0	0	0
94	2.2936	0	0	0	0	0	0	0
95	0	0	2.2936	0	0	0	0	0
96	2.0387	0.0112	0	0	0	0	0	0
97	0	0	1.5291	0	0	0	1.5291	0
98	0	0	0	1.2742	0	0	0	0
99	0	0.2321	1.0769	0	0	0	2.5484	0
100	0	0	0	39.134	0	0	0	0
101	0	0	0	5.1066	0	0	0	0
102	0	0	25.064	11.073	23.445	0	37.334	31.753
103	0.163	0.1166	0.4663	0.268	0.1862	0	0	0
104	0.2603	0.3793	0.8313	2.7833	0	0	0	0
105	31.412	0	9.4485	7.4505	0	0	0	0
106	0	0	0.1862	0.3725	0	0	0	0
107	0	0	0	0	5.2886	4.2983	2.7684	6.94
108	0	0	0.1055	0	0	0	0	0
109	21.727	0	0	0.1055	22.086	0	7.6453	0
110	0	0	83.106	0	0	0	0	0
111	53.171	11.328	17.552	5.9751	43.176	18.135	22.866	34.666
112	18.441	0	10.753	5.8448	0	0	14.271	0
113	0	0	10.753	0	0	0	55.046	0
114	0	112.13	0	0	0	0	0	50.714
115	0	0.0927	0	0	0	0	0	0
116	0	0.2647	0	0	0	0	0	0
117	0.3271	0.2811	0	0	0.8985	0.5646	0.0061	0
118	0.0083	0	0	0	0	0	0	0
119	0	0	0	0	1.0194	0.005	0.4005	3.7074
120	0	0.0374	0	0	0	0	0	0
121	0	0.725	0.232	0.4452	0	0	0.2307	0
122	0.3785	0	0	0.2163	0.4326	0.2163	0	0.4326
123	1.0373	2.8908	0.278	1.5711	11.134	16.636	2.7023	1.9345
124	4.135	0	0	17.715	0	1.2156	0	0
125	0.1388	0.43	0.599	0.2262	82.509	1.141	2.6317	2.47
126	0.8767	0.4383	1.01	0	0	0.4383	0.8767	0
127	0	0	0.0076	0	15.8	0	0	15.291

code	CC1	SC1	CM1	SM1	CC2	SC2	CM2	SM2
128	0	0.4613	0	0.3	0	25.484	0	0.9325
129	0	0.04	0	0	0	0	0	0.04
130	0	0	0	0	0	2.8276	0.025	0.04
131	0.5379	0	0.4922	0.5547	0	0.2088	16.739	0
132	0	0	0.3716	0	0	0	0	0.105
133	0.0244	0	0	0	0	0	0	4.105
134	0	0	0	0	0	0	1.2742	0
135	0	0.8806	0	0	0	0.6183	0	0
136	0.1157	0.2894	0.1157	0.4051	0.1157	0.1157	0	0.695
137	0	0.0636	0.8806	1.8118	0.2607	3.1636	0.8919	3.5678
138	0	4.9548	0	3.9076	4.9548	0	0	0
139	0	0	0.08	0	0	0	0	0.5097
140	3.1035	0	8.1549	0	0	0	0	0
141	0	0.265	0.53	0	0	0.1	0	0
142	0.0792	0	0	0	0	0	0	0
143	0	0	0.0818	0.2455	0	0	0	0
144	0.0237	0.075	0.0469	0.0505	0.005	0	0	2.1187
145	0.0025	0	0.0005	0	0	0	0	0
146	0	0.0181	0	0	0	0	0	0
147	0	2.9655	0	0	0	0	3.3398	5.3522
148	0	0	0	0	0	2.2936	2.0387	0
149	0	0.8995	0.0009	0	1.0194	5.0968	0	0
150	0.0975	0	0	0	0	0	0	0
151	8.6646	0	0	0	0	0	0	0
152	0	0.0087	1.3066	0	0.2848	0	0.0005	0
153	0	2.0387	0	0	0	13.507	0	13.383
154	0.0084	0.978	0.7966	1.0194	2.0387	2.6836	0	6.6259
155	0	0	1.4504	0	0	0	4.0775	0
156	0	2.0387	0	0	0	0.6331	0.051	0
157	0	0	7.6453	0	0	0	0	0
158	0	0	0.1585	0	0	0	0	0
159	0	0	0	0	0	0	47.91	0
160	0	0	0	0	0	0	3.0581	0
161	0	0	0	0	0	0	2.0387	0
162	0	71.865	0	0	0	0	0	0
163	0	12.232	0	0	0	0	0	0
164	0	10.703	37.717	0	0	0	0	6.6259
165	0	0	0	0	9.7483	0	0	0
166	0	38.736	0	0	0	41.794	0	21.407
167	0	57.797	6.4537	0	0	7.2751	0	0
168	0	5.9123	0	0	0	0.4077	0	0
169	0	0	0	0	0	43.833	0	25.994
170	0	101.6	260.45	64.73	9.1743	65.749	45.362	65.24
171	0	16.147	1.7329	0	0	18.349	5.0968	0
172	0	0	1.0475	0	0	0	0	0
173	0	0	0	277.78	0	0	0	0
174	63.965	0	0	45.362	0	0	0	0
175	0	0	0	0	114.17	55.046	0	0
176	229.87	0	0	208.46	0	0	0	0
177	0	0	0	0	0	0	35.168	0
178	0	2.8033	1.5291	0	0	8.1549	0	7.6453
179	0	0	0	0	0	0	46.126	0
180	0	536.19	0	0	0	0	5180.4	0
181	21.916	0	7.1356	0	0	0	36.697	0
182	33.639	0	82.569	0	148.83	6.1162	61.672	0

code	CC1	SC1	CM1	SM1	CC2	SC2	CM2	SM2
183	0	22.171	34.149	0	0	0	0	0
184	419.72	111.96	75.79	172.27	398.06	48.675	94.648	48.08
185	69.827	0	0	0	0	8.6646	0	0
186	197.5	0	87.156	0	0	16.31	0	21.407
187	0	0	0	0	0	4.4173	0	0
188	0	0	0	0	0	0	2.2086	0
189	0	1.7839	0	0	0	0	0	2.421
190	3.0581	0	4.5872	3.0581	0	5.0968	0	9.1743
191	0	4.0775	4.3323	0	0	6.8807	2.5484	0
192	2.8033	2.8033	2.8033	0	0	0	0	0
193	28.542	0	0	0	0	0	0	0
194	0	0	0	0.7981	0	0	0	0
195	0	0.5097	0	0	0	3.9501	0.0275	0
196	0	0	0	0	0	12.742	0	0
197	0	0	0.0655	4.5872	0	30.071	34.703	1.187
198	0	0	0	11.251	0	0	0	0
199	0	0	0.152	0	0	0	0	0
200	0	0	2.1411	0	0	0	0	0
201	0	2.0553	0	0	0	0	0	0
202	0	2.5484	0	0	0	7.1356	0	0
203	18.858	0	0	0	0	0	0	0
204	47.91	47.146	154.43	0	0	0	69.827	0
205	0	25.994	0	0	0	0	0	0
206	0.1742	0	2.7916	17.839	0	0	0	0
207	0	1108.1	0	0	0	0	0	0
208	0	0	0	0	0	0	13.507	0
209	0	0	3.3129	0	0	0	0	0
210	0	0	0	0	39.246	0	0	0
211	0	0	0	0	0	0	0	27.523
212	0	0	55.046	0	0	0	0	53.007
213	0	44.088	0	0	0	0	0	25.484
214	0	0	0	0.5097	0	0	0	0
215	0	0	1.0194	0	0	0	0	0
216	0	0	0.125	2.5484	0	0	0	0
217	0	0	11.723	0	0	0	0	0
218	0.7	0	0	0	0	0	0	0
219	0	0	0.3646	0	0	0	0	0
220	0	0	0	0.1855	0	0	0	0
221	0.3833	0	11.953	0.345	0	0	23.445	0
222	9.8678	22.868	12.487	0	10.703	8.5966	0	0
223	0	0	0	13.507	0	9.4292	0	0
224	0	0	0	1.0194	1.0194	0	0	0
225	0	0	0	0	5.72	0	0	0
226	0	1.0194	0	0	0	0	0	0
227	0	0	0	0	4.0775	0	0	0
228	0	25.484	0	29.052	0	0	0	0
229	0.775	0	0	0	0	0	0	0
230	0	0	0	13.507	0	17.329	0	0
231	0	0	4.0775	0	0	0	0.5097	0
232	0	0	0	0	0.84	0	0	0
233	0	0	0	0	0	1.0194	0.5097	0.5097
234	14.271	0	0	0	0	0	0	0
235	0	0	0	0	0.1808	0.7956	0	0
236	0	0	0.6313	0.05	0	0	0	0
237	0	2.775	0.485	0	0	0	0	0

code	CC1	SC1	CM1	SM1	CC2	SC2	CM2	SM2
293	0	0	0	0	0	0	0.175	0
294	0.225	0	0.35	0	0	0	0	0
295	0	0	0.15	0	0	0	0	0
296	0	0	0.025	0	0	0	0	0
297	0	0	0.025	0.5097	0	0	0	0
298	0	0	0.05	0.05	0	0	0.05	0
299	0.05	0	0	0	0	0	0.15	0
300	0.05	0.05	0.075	0	0.05	0.05	0	0.035
301	0	0	0.1699	0.2039	0.2623	0.0929	0.0576	1.228
302	0	0	0	0	0	0	0.1933	0
303	0	0	0	0	0	0.025	0	0.15
304	0	0	0.7895	0	0.075	0.3875	0.075	0
305	0	147.49	132.74	88.496	0	147.49	132.74	88.496
306	0.1681	0.0375	0.1841	0.1275	0.1712	0.0703	0.2081	0.0792
307	0.1681	0.0375	0.1841	0.1275	0.1712	0.0703	0.2081	0.0792
308	0	0	0	0	0	0	0.175	0
309	0.1	0	0	0	0	0.224	0.0216	0
310	0	0	0.06	0	0	0	0.2425	0.06
311	0	0.5097	0.5097	0	0	0	0.022	0
312	16.519	49.558	12.389	0	16.519	49.558	12.389	0
313	0	0	24.779	0	0	0	24.779	0
314	0.15	0	0	0	0	0	0	0
315	4.5	0	0	1.35	0	0	0	0
316	0.0125	0.0167	0	0.0125	0	0	0	0
317	0	0.025	0	0	0	0	0	0
318	0	0	0	0	0	0	0.025	0
319	0.8674	0.9769	0.0235	0.0155	1.0194	0	0.122	0.3562
320	0	1.15	1.4688	0	0	1.5	0	0.9925
321	0	0	0.5	0	0	0	0.4	0.6333
322	0.6	1.2719	0.3813	0.6	0	0	0	0
323	0	0	0	0	0	0	0.075	0
324	0.85	0	2.4	0	0	0	0	0
325	0	0	0	0	0	0.575	1.0375	0
326	0	0	0	0	0.2	0	0	0
327	0	0	0	0	1	0	0	0
328	2.15	0	0	2.35	0.675	0	0	1.95
329	0	0	0.85	0	0	0	0	0
330	0.0385	0	0	0	0	0	0	0
331	0.09	0	0	0	0	0	0	0
332	177.75	0	30.581	0	251.33	0.45	0	0
333	0	0	2.95	0	0	0	0	0
334	0.925	0	0	0.775	0	0	0	0
335	0	0	0	0.2	0	0	0	0
336	0	0	0	0	0	0	0.45	0
337	0	0	0	0	0	3.025	0.235	0
338	0.145	0	0	0	0	2.325	0.7667	1.75
339	0	5.8	0	0	0	0	0	0
340	0	0	0	0	0	0	0.525	0
341	1.1	0	0	0	0	0	3.025	5.65
342	0	0	0	0	0	0.05	0	0
343	0	0	88.496	0	0	0	88.496	0
344	0.295	0	0.4425	0.6637	0	0	0	0
345	0	0	0	0.225	0	0	0	0
346	0.125	0.3063	0.125	0.4625	2.5484	0.847	0	0.125
347	0	0	0	0.025	0	0	0	0

code	CC1	SC1	CM1	SM1	CC2	SC2	CM2	SM2
348	0	0	0.1	0	0.3	0.3	0	0.22
349	0	0	0	0	0	0	0	0.3
350	0	0	0	0	0.7	0	0	0
351	0	0	3.807	0	0	0	0	0
352	8.1723	0	11.505	10.409	0	0	0	2.7637
353	0	0	0	0	17.839	0	0	0
354	0	0	0	0	0	1.767	0	0
355	0	0	11.921	0	15.895	7.9474	0	27.816
356	0	0	0	0	0	7.9474	7.9781	0
357	10.398	0	8.6646	0.55	13.476	0	24.21	0
358	0.5097	0	0	0	0	0	0	0
359	0	0.475	0	0	0	0	0	0
360	4.7097	9.684	0	0.13	0	0	0	0
361	0	0	0	0	0	12.742	0	0
362	0.005	0	0.1383	0	0	0	0	0
363	0	0	0	0	0	0	0	0.505
364	0	0	0	0.575	0	0	0	0
365	4.253	0	8.1538	0.3977	16.216	8.1082	0.3977	0
366	0	0	0	0.8775	0	0	0	0
367	0.004	0.2239	0.02	0.02	0	0	0	0
368	0.39	0.585	0	0	0	0	0	0
369	1.1179	0.8235	1.0419	0.8235	0	2.425	0	2.2587
370	1.7475	0	0	0	0	0	0	0
371	1.0194	0	0	0	0.1321	0.5143	0	0
372	2.8878	0	0	0	0	0	0	0
373	0	0	0.6289	0	0	0	0	0
374	0	0	0	0	0.4352	0	0	0
375	0.0296	0	0	0	0	0	0	0
376	0	0	0	0	0	0.6	0	0.575
377	0.025	0	0	0	0	0	0	0
378	0	0	0	0	0.2984	0	0	0
379	0	2.5484	0	0	0	1.5291	0	0.8
380	23.537	2.5482	7.2545	0.8922	2.2426	3.8018	1.4679	0.8147
381	0.35	0	0	0	0	0	0	0
382	0	0	2.925	2.225	0	0	1.275	0
383	0	0	0	0	0	0	0	0.775
384	0	0	0	0	0	0	2.2969	2.4375
385	0	0	0	0	0	0	0	0.07
386	1.2052	0.4444	0.075	0	0.2219	0.6024	0.932	2.518
387	0	0	0	0	9.4292	0	4.5823	0
388	0	0.6626	0.1529	0.1274	0	0.1529	0.1044	0.2064
389	0	0	4.7	0	0	0	0	0
390	0	0.775	0	0	0	0	0.825	0
391	0.175	0	0	0	0	0	0	0
392	0	0.3058	0	0	0	0	0	0
393	0	0	0	0	0	0.0166	0	0
394	0	0	0	0.008	0	0	0	0
395	0	0	0	0	0.8155	0.4077	0.4077	0
396	0	0	0	0	0	0	0	0.0224
397	0	0	0.0795	0	0	0	0	0
398	0	0	0.0561	0	0	0	0	0
399	0	0.07	0	0	0	0	0	0
400	0	0	0	0	0	0.07	0	38.736
401	0	0	2.5484	0	0	3.5678	0	7.1356
402	0.325	0.33	0.649	0.0583	0.3188	0.7	0.575	0.125

code	CC1	SC1	CM1	SM1	CC2	SC2	CM2	SM2
462	0	0.5778	0	0.3611	0	0.5778	0	0.3611
463	0.9524	0	1.25	0	0.9524	0	1.25	0
464	8.2547	14.957	8.2547	14.957	8.2547	14.957	8.2547	14.957
465	23.529	23.529	23.529	23.529	23.529	23.529	23.529	23.529
466	5.8824	5.8824	5.8824	5.8824	5.8824	5.8824	5.8824	5.8824
44	0	0	0	0	0	0	50	0
45	0	0	0	100	100	0	0	0
46	0	0	0	0	0	0	150	0
47	0	0	0	0	0	0	10	0
457	0	1.7778	0	0.6944	0	1.7778	0	0.6944
458	0	4.4444	0	2.7778	0	4.4444	0	2.7778
459	5.8824	5.8824	5.8824	5.8824	5.8824	5.8824	5.8824	5.8824
460	0	0	0	2.7778	0	0	0	2.7778

IV Phylogenetic constraints and adaptation explain food-web structure¹

Food webs are descriptions of who eats whom in an ecosystem. Although extremely complex and variable, their structure possesses basic regularities¹⁻⁶. A fascinating question is to find a simple model capturing the underlying processes behind these repeatable patterns. Until now, two models have been devised for the description of trophic interactions within a natural community^{7,8}. Both are essentially based on the concept of ecological niche, with the consumers organized along a single niche dimension; for example, prey size^{8,9}. Unfortunately, they fail to describe adequately recent and high-quality data. Here, we propose a new model built on the hypothesis that any species' diet is the consequence of phylogenetic constraints and adaptation. Simple rules incorporating both concepts yield food webs whose structure is very close to real data. Consumers are organized in groups forming a nested hierarchy, which better reflects the complexity and multidimensionality of most natural systems.

A central issue in ecology is to uncover the basic determinants of the distribution of trophic interactions among the members of natural communities⁹. The architecture of interactions affects the stability properties of dynamical models of food webs^{2,10,11}. Therefore, a full understanding of dynamic ecosystems cannot be achieved at the economy of assuming a static structure of food webs, as was the case in the pioneering works on stability and complexity that considered interactions to be random^{12,13}. It has been shown unambiguously that real food webs are different from randomly connected networks, and that such a null-model cannot account for the observed properties of the highest quality food webs available^{6,8}. The structural models of trophic interactions proposed so far are the cascade model⁷ and the niche model⁸. The former assumes that species are ranked from 1 to S (total number of species), and that a consumer preys only on species of lower rank, with probability $P=2SC/(S-1)$ (directed connectance $C=L/S^2$, where L is the total number of trophic links). The niche model orders the species according to a randomly drawn 'niche value', n_i ($0 \leq n_i \leq 1$). A consumer eats all species falling into a range whose centre c_i is randomly chosen, with $c_i < n_i$. This restricts diets to be contiguous (Fig. 1a). Contiguity reflects the ecological assumption that diets can be arranged along one niche dimension.

¹ Chapter in press: Cattin M.F., Bersier L.F., Banašek-Richter C., Baltensperger R., Gabriel J.P. *Nature*.

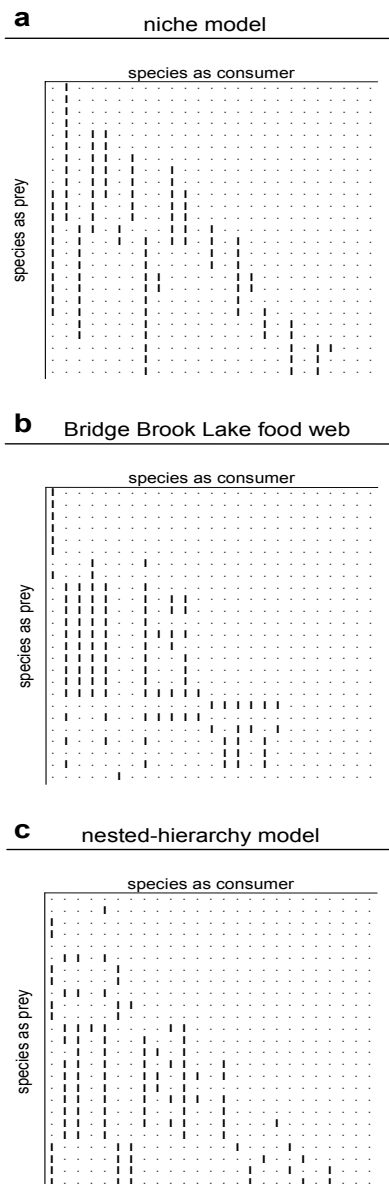


Fig. 1. Comparison of one simulation of **a**, the niche model and of **c**, the nested hierarchy model, with respect to **b**, a real food web (Bridge Brook Lake⁴). The food-web matrix depicts the trophic relationships, a "I" indicating that the species in the column consumes the species in the row (columns and rows contain the same species).

Whereas the cascade model fails to describe real data, the niche model closely predicts properties of recent high-quality food webs⁸. However, it does not totally account for the observed patterns. The model is known to produce only interval food webs (Fig. 2a,b). These interval webs possess the intriguing characteristic that the feeding relationships between consumers can be represented in one dimension^{1,14}, thought to correspond to a body size hierarchy⁹. Yet, non-interval food webs characterize recent high-quality data⁸. A more fundamental problem is that a key assumption of the niche model, contiguity of diets, is not observed in real food webs. By constraining consumers to eat all species in a range, the niche model entails no gap in diets for a suitable ordering of the prey (no gap in columns of Fig. 1a). In a food-web matrix, it is often computationally impracticable to find the prey sequence that would yield the minimum number of gaps. However, an irreducible gap can occur with at least three non-monophagous consumers (a triplet; see Fig. 2c). Consequently, we propose a new property of food-web structure—the level of diet discontinuity, D_{diet} —

defined as the proportion of triplets with an irreducible gap over the number of possible triplets. The niche model predicts D_{diet} to equal 0. In seven of the largest and highest quality empirical food webs (see Methods), the mean of D_{diet} is 0.18, a figure significantly different from 0 ($P=0.006$, one-tailed, one-sample t -test; Table 1).

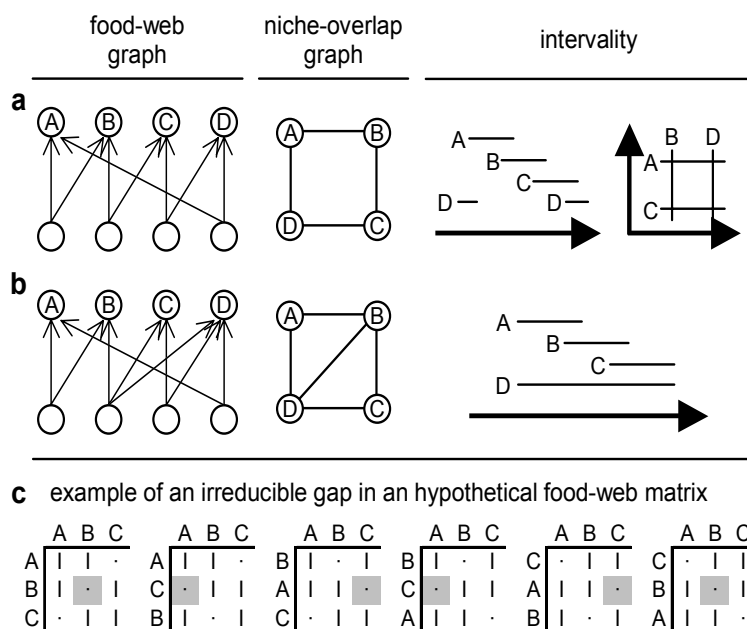


Fig. 2. Hypothetical food webs illustrating **a-b**, chordless cycles and intervality, and **c**, irreducible gaps. **a-b**, Food-web graph: circles are species and arrows are flows; A to D are consumers. The niche-overlap graph is an undirected graph where consumers sharing prey are connected. Under “intervality”, graphs depict consumers as segments; segments overlap if consumers share prey. **a**, a chordless and non-interval food web. The niche-overlap graph is chordless because no edge links A to C and/or B to D; the food web is non-interval: consumer D (broken line) cannot be placed in one dimension, because it overlaps with A and C, but not with B; two dimensions are needed. **b**, a non-chordless and interval food web.

These difficulties prompted us to take an evolutionary perspective of the basic ecological determinants of trophic interactions. Typically, a consumer’s diet is constrained by its phylogenetic origin¹⁵. For example, all warblers of the *Phylloscopus* genus possess a beak suited to prey on insects; all locusts of the Acrididae family have mouthparts and an alimentary tract suited for plant material. To substantiate the connection between phylogenetic origin and diet, we compared the matrices of trophic and taxonomic similarity for five empirical food webs by Mantel tests¹⁶ (see Methods). There was a strong relationship (all P -values <0.001), indicating that the distribution of trophic interactions is indeed related to the structure imposed by the phylogeny of the species forming the community.

However, the variability seen in the trophic relations between species cannot be explained fully by phylogenetic constraints. Species have to adapt to varying environments in order to survive, diverging from close relatives in their behaviour, and possibly innovating by using new food sources. Within this framework for example, the diet of New Guinea's fruit pigeons¹⁷ may be seen as constrained by the type of beak and digestive system characteristic of Columbiformes, and the partitioning of fruit size by adaptation to the biotic environment. Dietary shifts also occur frequently, especially in higher animals that are known to be opportunistic. In accordance with the macroevolutionary theory¹⁸, we feel that both phylogenetic constraints and adaptation are the essential determinants of the distribution of trophic interactions in any community.

We devised simple rules to generate food-web matrices according to both concepts. A food-web matrix is a S -by- S matrix with species as prey in rows and the same list of species as consumers in columns, with a '1' indicating that the species in the column consumes the species in the row (see Fig. 1). As with the cascade and niche models, parameters S and L are needed. We followed ref. 8 to set the number of links per consumer, which requires species to be ordered according to their 'niche value'; species with the smallest niche value tend to have the smallest number of prey (see Methods). The trophic links are attributed to consumers in a two-stage process, starting with the smallest niche value. In stage one, prey species of consumer i is randomly chosen among species with rank $< i$. Depending on this randomly chosen prey j , two cases are possible: (1) prey j has no consumer and therefore the next prey of consumer i will again be randomly attributed (with rank of prey $< i$); (2) prey j already has one or more consumers and therefore consumer i joins the group of species j 's consumers (that is, all consumers sharing at least one prey, with at least one consumer of this group feeding on j), and the next prey of consumer i is then randomly chosen among the set of prey of this group. If however the number of prey in the group is too small for choosing all remaining prey of consumer i , the remaining prey are again (randomly) chosen among prey without consumers (with rank of prey $< i$). The second stage is needed if prey still cannot be attributed; remaining prey of consumers for which prey could not be attributed in stage 1 are randomly chosen (prey species can have rank $\leq i$).

By creating groups of consumers, stage one (2) expresses the part in food-web organization that is determined by phylogenetic constraints. Links attributed to species free of consumers, and links distributed randomly in the second stage, render the adaptation of consumers to new prey. In forcing consumers to form various trophic groups, our 'nested-hierarchy model' escapes the one-dimensional nature of former models, and better reflects the kind of hierarchies emanating from the phylogenetic structure of the community.

We analysed 12 properties of food webs generated by the niche model as opposed to food webs generated by our model (see Methods). The results of 1,000 simulations of each

model for webs with $S=20-100$ ($S=20-50$ for computer-intensive properties) and $C=0.11$ (ref.19) show that both models yield quite similar results (Fig. 3). When compared with the seven reference food webs, we observe that the niche model performs slightly better for five properties (Gen_{sd} , M_{sim} , Lo , Can_{sp} , O), that our model is better for four properties (B , Vul_{sd} , Ch_{mean} , Ch_{log}), and that both models are equal for T , I and Ch_{sd} (Wilcoxon paired-sample tests, Table 1; see Methods for definitions). In sum, our model performs as well as the niche model—itsself outperforming the cascade model by one order of magnitude—in the prediction of these standard food-web descriptors.

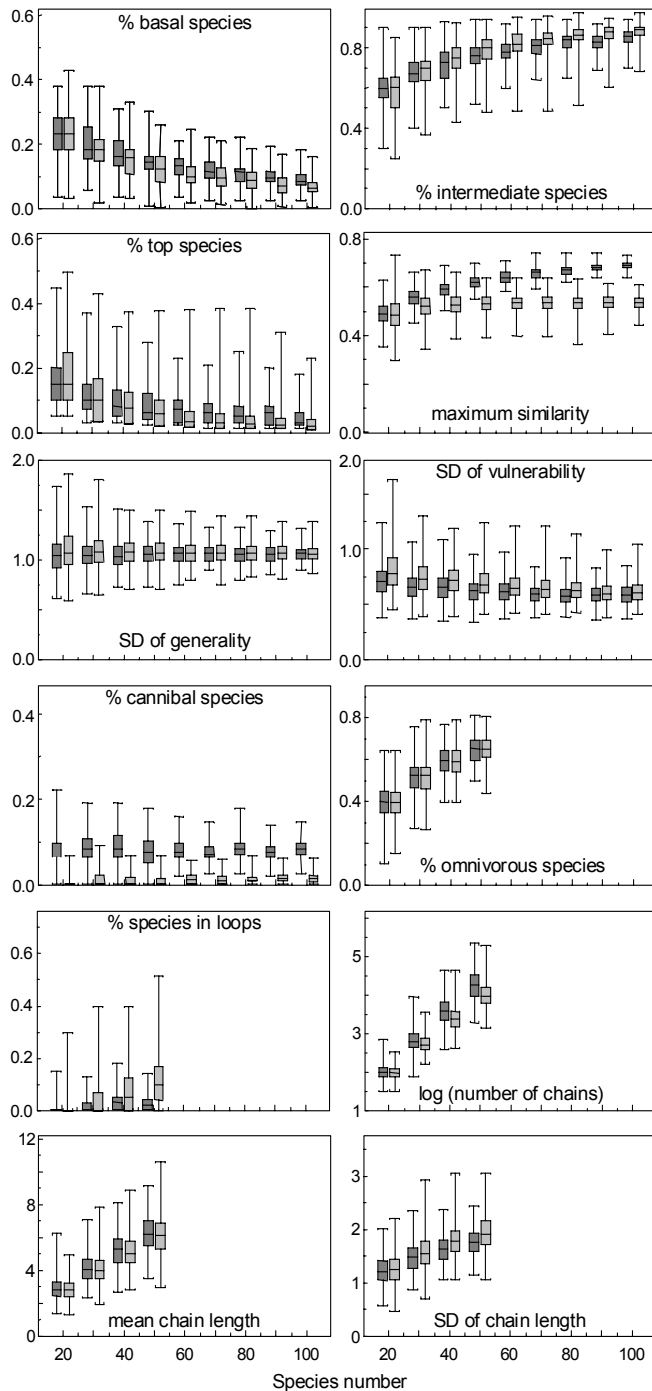


Fig. 3. Comparison of 12 properties (see Methods) of food webs generated by the niche model (dark grey boxes) and the nested-hierarchy model (light grey boxes).

The nested-hierarchy model surpasses the niche model for two additional properties: D_{diet} and the number of chordless cycles, Cy_4 (Table 1). The latter is closely linked to intervality, as interval food webs have no chordless cycles² (Fig. 2); Cy_4 may thus be thought of as the degree of departure from intervality (that is, from the possibility of ordering the consumers along a single dimension). Finally, the nested-hierarchy model generates food-web matrices whose global structure is close to the observed ones (Fig. 1c).

Table 1 Comparison of properties for seven food webs

Property	Skipwith Pond		Little Rock Lake		Bridge Brook Lake		Chesapeake Bay		Ythan Estuary		Coachella Desert		St Martin Island								
T	0.06	[0.04]	0.08	0.05	[0]	0.03	0.10	[0]	0.10	0.14	[0.28]	0.15	0.08	[0.38]	0.07	0.06	[0]	0.08	0.09	[0.17]	0.08
I	0.85	[0.92]	0.82	0.85	[0.87]	0.88	0.73	[0.68]	0.74	0.60	[0.62]	0.59	0.74	[0.53]	0.77	0.86	[0.90]	0.83	0.75	[0.69]	0.77
B	0.09	[0.04]	0.10	0.10	[0.13]	0.08	0.17	[0.32]	0.16	0.26	[0.10]	0.26	0.18	[0.09]	0.17	0.09	[0.10]	0.08	0.17	[0.14]	0.15
Gen_{sd}	0.76	[0.92]	0.83	1.06	[1.40]	1.08	0.98	[1.09]	1.03	1.12	[0.71]	1.17	1.17	[1.16]	1.18	0.81	[0.73]	0.83	1.06	[1.02]	1.09
Vul_{sd}	0.55	[0.54]	0.59	0.59	[0.57]	0.59	0.63	[0.61]	0.72	0.73	[1.03]	0.80	0.66	[1.40]	0.71	0.53	[0.60]	0.60	0.64	[0.78]	0.71
M_{sim}	0.73	[0.76]	0.67	0.69	[0.76]	0.54	0.61	[0.71]	0.56	0.48	[0.34]	0.48	0.58	[0.50]	0.50	0.74	[0.72]	0.67	0.62	[0.54]	0.53
Ch_{mean}	6.23	[4.81]	5.38				4.86	[2.55]	4.30	3.28	[2.77]	3.30	6.39	[4.89]	6.94	6.95	[7.18]	5.78	5.76	[4.20]	5.62
Ch_{sd}	1.56	[1.32]	1.58				1.51	[0.76]	1.52	1.36	[1.14]	1.42	1.89	[1.50]	2.17	1.68	[1.89]	1.64	1.65	[1.30]	1.82
Ch_{log}	4.21	[3.52]	3.70				3.20	[2.62]	2.90	2.35	[2.11]	2.32	4.39	[3.99]	4.38	4.62	[4.90]	4.04	3.96	[3.52]	3.71
Lo	0.25	[0.12]	0.40				0.05	[0]	0.13	0.00	[0.24]	0.02	0.01	[0]	0.06	0.26	[0]	0.42	0.03	[0]	0.11
Can_{sp}	0.43	[0.32]	0.10	0.14	[0.15]	0.03	0.21	[0.12]	0.03	0.08	[0]	0.00	0.07	[0.04]	0.01	0.44	[0.66]	0.09	0.13	[0]	0.02
O	0.77	[0.6]	0.76				0.61	[0.36]	0.60	0.42	[0.38]	0.41	0.61	[0.53]	0.61	0.75	[0.79]	0.78	0.63	[0.60]	0.63
Cy^4	0	[0]	0	0	[639]	626	0	[0]	0	0	[0]	0	0	[206]	18	0	[36]	1	0	[226]	6
D_{diet}	0	[0.35]	0.16	0	[0.08]	0.09	0	[0.004]	0.09	0	[0.08]	0.02	0	[0.32]	0.02	0	[0.28]	0.17	0	[0.17]	0.07

For each food web, empirical values are in brackets, means (medians for Cy_4) for the niche model are on the left, those for the nested-hierarchy model on the right. See Methods for a description of properties and of food webs. Little Rock Lake food web is too large for Ch_{log} , Ch_{sd} , Ch_{mean} , Lo and O to be computed in a reasonable length of time.

There are surely other conceivable ways in which to include phylogenetic constraints and adaptation; the one we devised was for us the most intuitive and most parsimonious. The fact that such simple rules are able to faithfully reproduce objects as complex as food webs is a strong hint at their usefulness; for example, as a roadmap for the interactions in dynamical models. What we perceive to be of higher importance than details of model construction are the processes behind the nested-hierarchy model. We have shown how phylogeny is intimately linked to trophic structure in natural communities, and how, once included in a model, it closely predicts observed patterns. When considering trophic links, body size is without doubt another constraint that will limit possible interactions²⁰. Yet body size varies widely within trophic groups, and the size distributions of different trophic groups can overlap extensively—simply think of the herbivores and carnivores in African savannahs.

As a consequence, body size is of secondary importance in explaining food-web structure when compared with phylogeny.

Compared with the niche and the cascade models, we impose a sequence in the attribution of links, because a consumer's diet will depend on the species already present. Accordingly, prey are first attributed to primary consumers, as expected in the course of community development. This sequential process is inspired by the niche-hierarchy model²¹, an assembly rule stating that species joining a community will be successful only if they compete within single guilds. For example, it would not be possible for a bird feeding on fruits and insects to enter a community if guilds of frugivores and insectivores are already present. The niche-hierarchy model will also generate nested hierarchies with groups defined by their feeding habits. In our model, we propose that this grouping is constrained by phylogeny, but we permit species to break the strict rule of the niche-hierarchy model by allowing consumers to prey on species outside their group. The niche-hierarchy model has recently been extended to explain patterns of species abundances²². An intriguing perspective would be to combine the niche-hierarchy with our nested-hierarchy model. It will offer a framework to get a sharper understanding of quantitative food webs, including the relationship between abundance, body size and trophic structure²⁰.

Methods

Data set

The food webs considered here and in ref. 8 are the following (N =total number of taxa, S =total number of trophic species, C =directed connectance): Skipwith pond²³ ($N=35$, $S=25$, $C=0.32$); Chesapeake Bay²⁴ ($N=33$, $S=31$, $C=0.072$); Ythan Estuary²⁵ ($N=92$, $S=79$, $C=0.061$); Coachella Valley²⁶ ($N=30$, $S=29$, $C=0.31$); St Martin Island²⁷ ($N=44$, $S=42$, $C=0.12$); Little Rock Lake²⁸ ($N=180$, $S=94$, $C=0.12$); and Bridge Brook Lake⁴ ($N=75$, $S=25$, $C=0.17$). A trophic species is defined as a set of taxa sharing the same prey and consumers⁸.

Mantel test

Trophic similarity between two species i and j was measured with the index of Jaccard²⁹; that is, as the number of prey and of consumers shared by i and j divided by the pair's total number of prey and consumers. To measure taxonomic similarity, we first ascribed to each taxon (for economy, we use the word 'species' in the text, but prey and consumers are often described at a coarser taxonomic level) its taxonomic membership. We used ten levels: (1) kingdom, (2) superphylum, (3) phylum, (4) subphylum, (5) class, (6) subclass/superorder, (7) order, (8) suborder/superfamily, (9) family, (10) genus. Taxonomic

similarity between two taxa i and j was measured as the value of the most precise common taxonomic level (for example, ten for two species of the same genus) divided by one plus the value of the most detailed level of any of both taxa. We performed a Mantel test¹⁶ to compare the matrices of trophic and taxonomic similarity of Skipwith pond, Chesapeake Bay, Ythan Estuary, Coachella Valley and St Martin Island. Real taxa and not trophic species were used. Little Rock Lake and Bridge Brook Lake were not considered because taxonomic information was used to infer trophic interactions.

Model

To determine the number of links per consumer l_i , we assigned each species a niche value n_i uniformly drawn from $[0,1]$ and sorted species according to their n_i in ascending order. Each l_i was obtained by multiplying n_i by a value drawn from $[0,1]$, using a β -distribution with expected value $2C$ and with $\alpha=1$ (see ref. 8). To obtain the desired L , each consumer's l_i was divided by the sum of l_i over all species and multiplied by L . If the resulting l_i exceeded $S-1$, we arbitrarily reduced it to $S-1$. To ensure at least one basal species, the species with the smallest n_i had no prey. For computational reasons, we imposed the presence of at least one top species (the species with the largest n_i has no consumer). We excluded webs with connectance less than 97% of the desired C , with disconnected species, or with species sharing the same consumers and prey.

Properties

The following 14 properties were calculated for each web: B , I , and T , the proportions of basal (without prey), intermediate (with both predators and prey) and top (without predators) species, respectively; Gen_{sd} and Vul_{sd} , the standard deviations (s.d.) of generality and vulnerability⁸, which measure the variation in prey and predator numbers per species, respectively; M_{sim} , the mean maximum similarity of a web, which is the average of all species' largest value for the trophic similarity; Can_{sp} , the proportion of cannibalistic species; O , the proportion of omnivores (that is, species that consume at least two species and have food chains of different lengths); Ch_{log} , the log of the number of food chains (a food chain is a linked path between any species to a basal species); Ch_{mean} and Ch_{sd} , the mean and the s.d. of food chain lengths; Lo , the proportion of species involved in loops other than cannibalistic loops (that is, parts of food chains that include the same species twice). Links involved in loops are ignored for the computation of Ch_{log} , Ch_{mean} , Ch_{sd} and O . The final two properties are Cy_4 , the number of chordless cycles of length four (see Fig. 2), and D_{diet} , the level of diet discontinuity, which measures the proportion of triplets of consumers whose prey cannot be ordered so that the three diets are fully contiguous.

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V Synthesis - Models and conservation: is there any connection?

Can models – and the nested-hierarchy model in particular – be useful for conservation issues? We demonstrated in this model the importance of phylogenetic constraints, i.e. taxonomy, for food-web structure. It indicates that species are not interchangeable, and that a role in the ecosystem disappears with the loss of a species, thus modifying the functioning of the community. The other important factor explaining food-web structure in our nested-hierarchy model is adaptation. The capacity of species to adjust to newly vacated niches is typically unknown and should be further studied. If species can adapt and take the role of a disappeared species, then ecosystems have the capacity to maintain their functioning despite biodiversity losses. The extent to which species can adapt is an important component of the resilience of ecosystems (Kondoh 2003). We can suppose that this replacement capacity depends on the taxonomic distance between the species lost and its potential substitute, i.e., it might be possible for a species of the same genus to take the function of a disappeared species, but this could be much more difficult for a more distant species in the same order. Consequently, the drastic changes affecting particular environments and leading to the disappearance of entire taxonomic groups – for example coral reefs (e.g. Gardner et al. 2003, Szmant 2002, Buddemeier 2001) – are a particularly dramatic example of changes affecting durably a food-web structure. Future research aimed at determining the relative importance of constraints and adaptation in the reaction of ecosystems to species extinctions would be of greatest interest. This topic could be studied experimentally by means of the construction of food webs comprising a sufficiently large number of species to be realistic, in which species with various taxonomic relatedness degrees would be removed each in turn. The reaction of the other species and of the functioning of the food web would be measured for each species loss.

The second connection between the nested-hierarchy model and conservation is a fundamental need of precise taxonomic descriptions of the taxa encountered. In food-web studies, both empirical and theoretical, species are often lumped. This choice has two origins. Firstly, taxa are sometimes identified only to a coarse level, because of identification difficulties. Secondly, trophic species (Cohen et al. 1990) are often considered, i.e. species sharing the same set of predators and prey are lumped. Our model shows that this concept is not appropriate, because of the importance of taxonomy for food-web structure. A good taxonomic expertise is needed in both conservation and food-web ecology.

In both topics tackled in this thesis – models and conservation – the importance of taxonomy is reinforced by the fact that we use here qualitative properties of food-webs, which have been shown to be sensitive to sampling effort (Goldwasser & Roughgarden 1997, Bersier et al. 1999, Martinez et al. 1999). It would be of greatest interest to propose

models based on quantitative descriptions of food webs and to study the impact of management on the quantitative properties (Bersier et al. 2002) of food webs. For applied ecology, it would also be interesting to determine the coarsest level of taxonomic resolution necessary to put in evidence changes due to management in the ecosystem functioning. We are aware of the huge investment necessary to accurately describe food webs with a high taxonomic resolution; a quantitative approach could alleviate this need, and consequently be more readily applicable in conservation studies.

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VI Summary

Food webs are descriptions of who eats whom in an ecosystem. We propose here two different approaches to this topic. Firstly, we describe an empirical study applied to the management of fens of the Grande Cariçaie (on the south bank of Lake Neuchâtel), a site of high value for nature conservation in Switzerland. Secondly, we introduce a new model explaining food-web structure, the nested-hierarchy model, which solves major problems encountered with former models.

Nearly 90% of the fenlands in Switzerland have been lost during the last century. They harbour a high number of endangered species. Presently, they are threatened by brushwood encroachment and terrestrialisation due to water regulation and draining. Mowing is a commonly used management technique to prevent this succession. This management practice is beneficial for floristic diversity, but its effects on arthropods are less well known. Here, we use two different complementary approaches to study the effect of mowing on two types of wet meadows. Firstly, we evaluate the impact of management by means of the comparison of a control and a two-year-old mown area. The results indicate that mowing reduces the less mobile spiders and species linked to litter or dead reeds, including rare species. Secondly, in order to measure the impact of mowing on the ecosystem structure and functioning, we adopt a food-web approach in the same wet meadows. Our results demonstrate that mowing has different consequences depending on the trophic group and level. It increases the total number of taxa, an increase particularly beneficial to species of the first trophic level. The impact on the third trophic level is hardly perceivable, because of the dominance of generalist feeders in this level. Intermediate species and particularly herbivores show the strongest change: mowing results in a shift towards more generalist herbivores and detritivores to the detriment of specialized species. This could be a particularly undesirable consequence of management.

In the second part, we introduce the nested-hierarchy model, which describes food-web structure. Though extremely complex and variable, their structure possesses basic regularities. Until now, two models have been devised for the description of trophic interactions within a natural community. Both are essentially based upon the concept of ecological niche, with the consumers organized along a single niche dimension, e.g., prey size. Unfortunately, they fail to describe adequately recent high-quality data. We propose here a new model built on the hypothesis that any species' diet is the consequence of phylogenetic constraints and adaptation. Simple rules incorporating both concepts yield food webs whose structure is very close to real data. Consumers are organized in groups forming a nested hierarchy, which better reflects the complexity and multidimensionality of most natural systems.

Our nested-hierarchy model emphasizes the role of phylogenetic constraints in food webs. It is an important element to be considered in the actual context of decrease in biodiversity. The relative impacts of taxonomy and adaptation in the reaction of ecosystems to species losses remains to be determined.

Résumé

Les réseaux trophiques sont des descriptions de qui mange qui dans un écosystème. Nous proposons ici deux approches différentes de ce sujet. La première décrit une étude empirique appliquée à la gestion de marais non-boisés de la Grande Cariçaie (rive sud du Lac de Neuchâtel), un site de grande valeur pour la conservation de la nature en Suisse. La deuxième introduit un nouveau modèle qui permet d'expliquer la structure des réseaux trophiques, le «nested-hierarchy model», et qui apporte une solution aux problèmes non résolus par les précédents modèles.

Plus de 90% des bas-marais de Suisse ont disparu depuis le siècle dernier. Ils abritent beaucoup d'espèces rares, mais sont actuellement menacés par la succession, que le drainage et la régulation du niveau des eaux favorisent. La fauche est un moyen de conservation souvent utilisé pour prévenir l'atterrissement et l'embuisonnement des prairies humides. Cette pratique est efficace pour le maintien de la diversité floristique, mais ses effets sur les arthropodes notamment sont moins bien connus. Nous proposons ici d'examiner l'effet de la fauche sur deux types de prairies humides, sous deux approches complémentaires. Nous évaluons tout d'abord l'impact des mesures de gestion sur les araignées, en comparant une zone témoin et une zone fauchée deux saisons auparavant. Les résultats indiquent que certaines espèces souffrent de l'entretien. Il s'agit des araignées les moins mobiles et d'espèces, notamment rares, liées à la litière ou aux roseaux morts. Ensuite, afin de mesurer l'impact de la fauche sur la structure et le fonctionnement de l'écosystème, nous adoptons une approche basée sur la comparaison des réseaux trophiques. Nos résultats montrent des effets différents selon les groupes et les niveaux trophiques. Le nombre total de taxons augmente, une augmentation qui profite particulièrement au premier niveau trophique. L'impact sur le troisième niveau trophique est à peine perceptible, en raison de la dominance d'espèces généralistes. Les espèces intermédiaires, et en particulier les herbivores subissent les effets les plus marqués: la fauche provoque un changement vers plus d'herbivores généralistes et moins de

spécialistes. Si ces résultats devaient être confirmés, ce serait une conséquence particulièrement négative des mesures d'entretien.

Nous introduisons ensuite le «nested-hierarchy model», qui décrit la structure des réseaux trophiques. Malgré leur complexité et leur variabilité, leur structure possède des régularités. Deux modèles ont été proposés jusqu'à maintenant pour la description des interactions trophiques dans les communautés naturelles. Tous deux sont essentiellement basés sur le concept de niche écologique, avec les consommateurs organisés le long d'une seule dimension, supposée correspondre à la taille des organismes. Ils ne décrivent malheureusement pas adéquatement des données récentes de très bonne qualité. Le nouveau modèle proposé ici est construit sur l'hypothèse que le régime alimentaire des espèces est le résultat de l'influence de deux facteurs: les contraintes phylogénétiques et l'adaptation. Des règles simples qui tiennent compte de ces deux concepts permettent de construire des réseaux trophiques dont la structure est très proche de celle des données réelles. Les consommateurs sont organisés en groupes qui forment une hiérarchie emboîtée, qui reflète mieux la complexité et la multidimensionnalité de la plupart des écosystèmes naturels.

Notre «nested-hierarchy model» souligne le rôle joué par les contraintes phylogénétiques dans la structure des réseaux trophiques. C'est un élément important à prendre en considération pour la conservation des espèces, dans le contexte actuel de diminution de la biodiversité. L'importance relative de la taxonomie et de l'adaptation dans la réaction des écosystèmes à des disparitions d'espèces reste à déterminer.