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

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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 2-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 2–4 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.
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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 Güsewell 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). Dithlogo 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. Decleer (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 3 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 of mowing on the vegetation (e.g. Buttler, 1987, 1992; Güsewell et al. 1998, 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, 1989). 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.
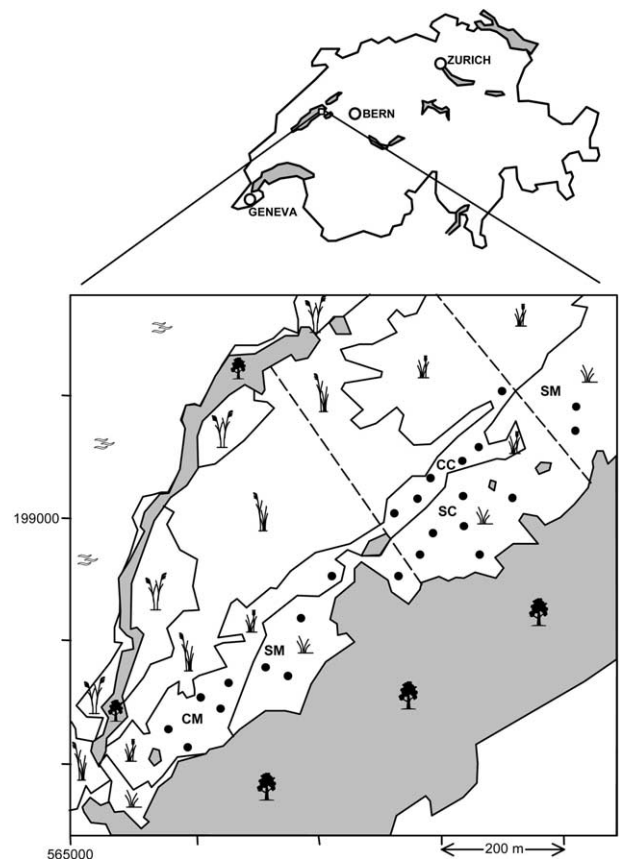

Fig. 1. Location of the study plots, in two vegetation types, mown triennially or unmanaged (control). CC, *Cladietum marisci*, control; CM, *Cladietum marisci*, mown; SC, *Orchio-Schoenetum nigricantis*, control; SM, *Orchio-Schoenetum nigricantis*, mown. Coordinates follow Swiss national grid. Dots 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 24 May to 21 July and 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). Spiders were sampled in each plot with cores measuring 50 cm diameter (~ 0.2 m^2) 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 analyses (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 [$\hat{z} = b_1 x + b_2 y + b_3 x^2 + b_4 xy + b_5 y^2 + b_6 x^3 + b_7 x^2 y + b_8 xy^2 + b_9 y^3$] 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 × 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 Decleer (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):

$$\text{DN} = e^H, \text{ with } H = -\sum_{i=1}^{S} p_i \cdot \ln p_i,$$

where p_i is the relative abundance of the ith species, and (4) Hurlbert's (1971) probability of an interspecific encounter:

$$\text{PIE} = \left(\frac{N}{N-1}\right) \cdot \left(1 - \sum_{i=1}^{S} \left(\frac{m_i}{N}\right)^2\right),$$

with N the total number of individuals, and m_i 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.

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/m^2.

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 and 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.

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 effect of mowing on diversity measures, specific taxa appeared to respond to this treatment.

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

	Treatment				Vegetation			
	Mown	Control	U	P	Cladietum	Schoenetum	U	P
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

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)

	Mown	Control	U	P
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[a]	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

[a] PIE, probability of an interspecific encounter.

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	P
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)

	Mown	Control	U	P
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*

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.

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/m^2) compared to densities typically found in natural and cultivated environments (50–150 individuals/m^2, 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, unpublished data). 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
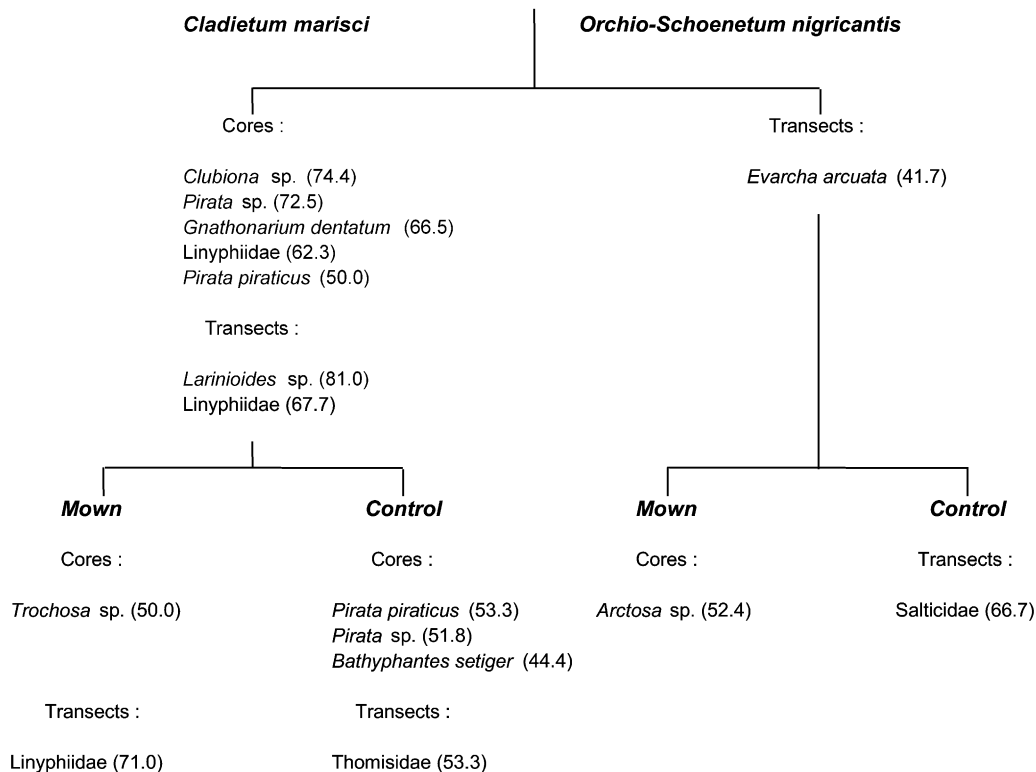
Cladietum marisci   **Orchio-Schoenetum nigricantis**

Cores :   Transects :

Clubiona sp. (74.4)   *Evarcha arcuata* (41.7)
Pirata sp. (72.5)
Gnathonarium dentatum (66.5)
Linyphiidae (62.3)
Pirata piraticus (50.0)

Transects :

Larinioides sp. (81.0)
Linyphiidae (67.7)

Mown   **Control**   **Mown**   **Control**

Cores :   Cores :   Cores :   Transects :

Trochosa sp. (50.0)   *Pirata piraticus* (53.3)   *Arctosa* sp. (52.4)   Salticidae (66.7)
                         Pirata sp. (51.8)
                         Bathyphantes setiger (44.4)

Transects :   Transects :

Linyphiidae (71.0)   Thomisidae (53.3)

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.

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 Decleer (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.

Decleer (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*, *Satilatlas 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 Cariçaie marshes, because of brushwood encroachment and succession.

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. Decleer, 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 c). This practice will end up in smaller surfaces of each vegetation type managed simultaneously, and provide zones
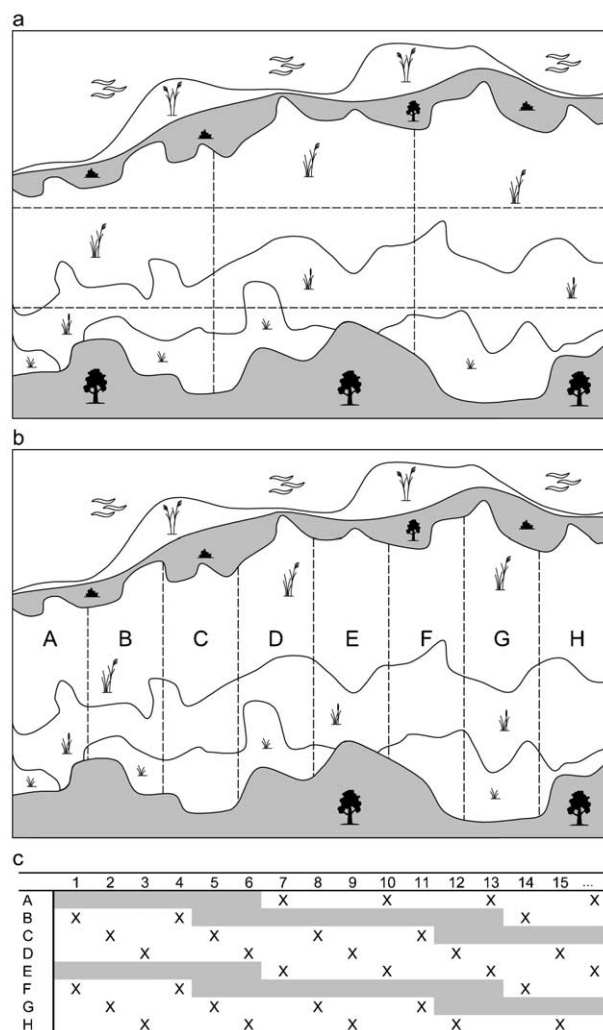

Fig. 3. Sketches of present (a) and proposed (b) management schemes for the mowing of the wet meadows in the Grande Cariçaie. Mowing sectors are delimited by broken lines. They are mown triennially in (a), and following a three years and a ten years period in (b). Proposed mowing regime is given in (c),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

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.

Appendix. Species list classified according to valuation categories

Ubiquitous species (UB): *Agraecina 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, Hahnia 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, Gongylidiellum 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, Satilatlas britteni, Tibellus maritimus.*

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

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