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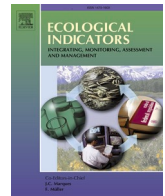
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Effects of environmental filtering on taxonomic and functional diversity patterns: When spiders and plants provide complementary information to water level management in the Seine estuary

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ABSTRACT

In the Seine estuary in northern France, many artificial structures limit the effect of the tide on associated alluvial zones. Consequently, this affects natural environmental filtering mechanisms linked to tidal regimes and water salinity, which directly influences the structure of organism assemblies in adjacent ecosystems. Here, we propose to study the influence of these filters' modifications on spiders and plants, two compartments recognized as complementary in terms of bioindication. However, this complementarity has only been studied to a limited extent and rarely in estuarine environments. To highlight this complementarity, we studied the taxonomic and functional patterns obtained across different topographical levels of two sites with contrasting water level managements. Moreover, particular attention was paid to the influence of the weight attributed to rare species (Q order) to shed light on processes affecting species dominance dynamics between taxa. Overall, spider communities appeared less influenced by environmental filtering than plants on both study sites, with taxonomic and functional diversity both demonstrating a low sensitivity to salinity. Spider community assemblies also demonstrated compositional shifts across study sites, mainly driven by changes in abundance and dominance. In contrast, plant communities appeared more sensitive to environmental constraints and water level management, with responses in terms of composition and species turnover rather than unbalanced abundance, suggesting responses at distinct spatial scales between plant and spider communities.

1. Introduction

Estuaries are transitional ecosystems between rivers and adjacent seas with high functional and conservation values worldwide (Pétillon et al., 2023). As a result of their geographical positioning, they have unique properties including a longitudinal salinity gradient due to the mix of fresh- and saltwater, as well as a lateral salinity and flooding gradient due to tidal and seasonal cycles (Desender & Maelfait, 1999). Because of the abiotic conditions' high daily and seasonal variability, estuaries cannot be defined as stable ecosystems but rather as an interconnected mosaic of changing habitats (Davidson, 1991). Despite this diversity of habitats, strong environmental filters generate in estuaries a low species richness with few species adapted to flooding and salinity, but with locally abundant populations of specialist species (McLusky &

Elliott, 2004; Meire et al., 2005). Therefore, estuaries act as a reserve habitat for unique fauna (Little, 2000). In addition, strong fluxes in biogeochemical cycles support numerous functions such as high primary production and carbon fixation (Costanza, Kemp, & Boynton, 1993). Due to this high functionality, estuaries provide various ecosystem services from a local scale (e.g., food production, tourism) to a more global and drastically essential level (e.g., nutrient cycling, climate regulation; Barbier et al., 2011; Heckbert et al., 2011; Thrush et al., 2014; Hambäck et al., 2023). For centuries, estuaries have been managed to optimize commercial shipping, fishing, and economic activity, resulting in high anthropogenic levels and degradation of riverbanks (Freeman et al., 2019). In addition, land reclamation for agricultural development reduces natural habitat areas and influences natural connectivity between habitats due to water level management (McLusky & Elliott, 2004).

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Furthermore, modifications of the natural flow of river systems primarily affect estuarine ecosystems by altering natural freshwater inputs (Gillanders & Kingsford, 2002). This, in turn, can result in modifications of salinity and temperature regimes, affecting the abundances, distribution, and composition of resident organisms (Kennish, 2002), and could lead to functional homogenization (Cavalcante et al., 2023). All these factors mainly affect the integrity of estuaries and the ecosystem services they provide. To reconcile economic development with the ecological integrity of estuaries, specific management strategies can be employed (Boerema & Meire, 2017). In order to develop management solutions, a thorough understanding of the target ecosystem is necessary, especially because land use issues are often site dependent.

The Seine estuary in northern France plays a major ecological role with an area of about 150 km² at high tide and an average discharge of 380 m³ s⁻¹ (Avoine, 1986). It also holds significant economic importance, with a large part of the French population, industry and agriculture activities concentrated along this stream (i.e., 16 million inhabitants and 40 % of the country's industry and agriculture) and supports 50 % of the national river traffic (Mouny et al., 1998; Lafite & Romána, 2001), with industrial sectors directly supported by the presence of the estuary (e.g. refined petroleum production: Beaumais & Laroutis 2007).

Consequently, the Seine estuary is a highly anthropized area with numerous artificial structures (dikes) limiting the effect of the tide on the associated alluvial zones. This results in a compartmentalized estuary with direct consequences on adjacent ecosystems, particularly through the modification of the lateral gradient of salinity and flooding. Consequently, natural transitions between subhalophilous meadows to freshwater meadows in alluvial zones have been modified in favor of agricultural freshwater environments (McLusky & Elliott, 2004). Additionally, the Seine estuary presents a national nature reserve including various land uses such as grazed and mowed areas with local hunting activities (Maison de l'Estuaire, 2023; Réserves Naturelles de France, 2023; Maison de l'Estuaire, 2018; ADREE, n.d). These land uses can locally interact with water level management and impact local organisms either directly (e.g., modification of arthropod communities by grazing and mowing; Pétilion et al., 2007) or indirectly because water level management must comply with the chosen land use types.

Ecological indicators are essential to highlight the impact of water level management, local land uses, and their interaction on the Seine estuary's biodiversity. Plants appear to be the most used bioindicators due to their high sensitivity to abiotic factors in general, including flooding and salinity stresses (McKee & Mendelssohn, 1989; Reed, 1995; Gough & Grace, 1998; Flindt et al., 1999). In the case of estuaries, plants have been proven to be relevant bioindicators (Weilhoefer, 2011). In order to better understand the link between water level management, land use, and biodiversity of alluvial zones, the use of several bioindicator taxa seems relevant. In many cases, spiders are neglected, even though their bioindication capacity is widely demonstrated (Pearce & Venier, 2006; Borchard et al., 2014). Additionally, they are present in high abundance in estuaries and are also able to indicate changes in flooding and salinity (Pétilion et al., 2003; Pétilion et al., 2014; Fournier et al., 2015; Ridel et al., 2021; Hambäck et al., 2022; Åhlén et al., 2024), but are still rarely used in this type of ecosystem (Desender & Maelfait, 1999; David et al., 2016). The coupled use of plants and spiders has the advantage of employing taxa from different trophic levels, exhibiting complementary responses to environmental changes (Lafage et al., 2015; 2019; Hacala et al., 2020). However, despite this apparent complementarity, few studies deal with these taxa as joint bioindicators (Hacala et al., 2024), and to our knowledge, no studies deal with exploring this complementarity in estuarine environments.

In order to properly assess ecosystem functionality, selecting complementary metrics that reflect variations in ecosystem processes as accurately as possible is an essential step. In fact, studying the local composition of community assemblages may reflect environmental filtering processes in both plants and spiders (Hacala et al., 2024).

Moreover, translating this composition into a diversity metric can provide a different way to understand the impact of environmental change on organisms (Santini et al., 2017). For example, species richness combined with Shannon and Simpson indices are traditionally used and considered complementary when assessing taxonomic diversity. These metrics can be unified using the Hill numbers of order q (Jost 2006; Tuomisto 2010; Chiarucci et al., 2011), based on Hill numbers (Hill 1973). This method takes the advantage, among others, of having direct links between Hill numbers and species compositional similarity. The order q determines the sensitivity of metrics to the relative frequencies of species, with all species are of equal weight when $q = 0$; species are weighted in proportion to their abundance when $q = 1$; and finally, abundant species are favored (and rare discounted) when $q = 2$ (see more details in Chao et al., 2014).

On the other hand, partitioning only taxonomic diversity metrics can lead to an incomplete assessment of the functionality of the ecosystem and/or target species (Devictor et al., 2010). To fill this gap, splitting diversity into taxonomic and functional facets can highlight more precise responses to environmental changes because species are considered not only as taxonomic units but also as organisms with their own functional characteristics (Petchey & Gaston, 2002; 2006). In many cases, taxonomic and functional diversity are linked because increasing species richness indirectly captures more functional traits (Pardo et al., 2017; Pavoine et al., 2013). However, the relationship between these metrics can provide new information for understanding biological processes like spatial variation (Devictor et al., 2010; Cadotte & Tucker, 2018). Therefore, combined diversity metrics can provide useful insights into links between biodiversity, ecosystem functions, and habitat characteristics such as environmental filtering (Díaz et al., 2007). To best describe functional diversity, numerous indices have been developed (Mouchet et al., 2010). However, when sampling small and mobile taxa such as spiders, a bias of under-sampling persists (Scharff et al., 2003), and few functional indices take this into account.

In order to properly compare the diversity of taxa without risks of under-sampling, methods have been developed to standardize sampling by ensuring its completeness (Chao et al., 2009; Chao & Jost, 2012). Chao indices have the advantage of partitioning taxonomic and functional diversity in a comparable way while still considering Q order (i.e., the weight given to rare species; Chao et al., 2009; 2014; Pavoine et al., 2016). Indeed, rare species can play a significant part in the overall functionality of the ecosystem (Lyons et al., 2005) because of their potential divergence from the rest of the community, supporting vulnerable functions (Mouillot et al., 2013; Jain et al., 2014). As a result, partitioning functional diversity into Q orders can highlight functional divergence between rare and abundant species, particularly in estuarine ecosystems where specialist species are in general highly abundant.

Here, we propose to investigate the influence of water management and local land uses on plants and spider assemblages and, more generally, to test the bioindicator complementarity of these taxa in estuarine environments using a case study in the Seine estuary. To our knowledge, this is the first time the bioindicator role of these taxa is explored simultaneously in a taxonomic and functional way in estuaries.

To achieve this objective, the following hypotheses will be tested:

- (1) Different patterns are expected between spider and plant assemblages due to high complementarity in the bioindicator capacity of these taxa (Lafage et al., 2015; Hacala et al., 2020; 2024). On the other hand, similar patterns are expected between these metrics for each taxon because in many cases taxonomic and functional diversity are linked (Pavoine et al., 2013; Hacala et al., 2021; Ridel et al., 2021).
- (2) Because salinity and flooding stress generally promote high abundance of specialist species (McLusky & Elliott, 2004; Meire et al., 2005), we expect an effect of Q order on taxonomic and functional diversity patterns on non-managed sites because of

higher constraints due to flooding, but not on managed sites for both taxa.

- (3) Due to water level management and local land uses, significant differences are expected between the composition of spider (Pétillon et al., 2003; Pétillon et al., 2014; Fournier et al., 2015; Ridel et al., 2021) and plant assemblages (McKee & Mendelssohn, 1989; Reed, 1995; Gough & Grace, 1998; Flindt et al., 1999) between sites. Additionally, differences are expected between topographical zones for each site (distance from the Seine on a lateral gradient), more pronounced on non-managed sites due to stronger environmental filtering linked to flooding and indicator species in line with both water level management and local land uses.
- (4) Finally, we expect an increasing proportion of halophilic species and individuals in the non-managed sites along the topographic gradient for spiders (Pétillon et al., 2008) and plants (Adam, 1981; Bertness & Ellison, 1987; Brewer & Grace, 1990; Wilson & Stubbs, 2012; Kim & Ohr, 2020) because of the natural flooding

gradient, contrasting with a stable proportion in non-managed sites linked to the absence of this flooding gradient.

2. Material and methods

2.1. Study sites

The study was conducted in the estuary of the river Seine (Le Havre, Normandy, France) (Fig. 1A, B), where three sites were selected for their differences in hydrological management type and lateral salinity gradient. Indeed, two of these sites are located on the north shore of the river and have water levels managed by valves and channels (called Managed 1 and Managed 2, abbreviated as M1 & M2), contrasting with the site located on the river's south shore which is not managed and therefore directly influenced by the tidal cycle (called Non-Managed and abbreviated as NM) (Fig. 1C). Additionally, the three study sites are positioned on a lateral gradient of proximity to the sea (and therefore theoretically a salinity gradient) with M2, M1, and NM ordered from

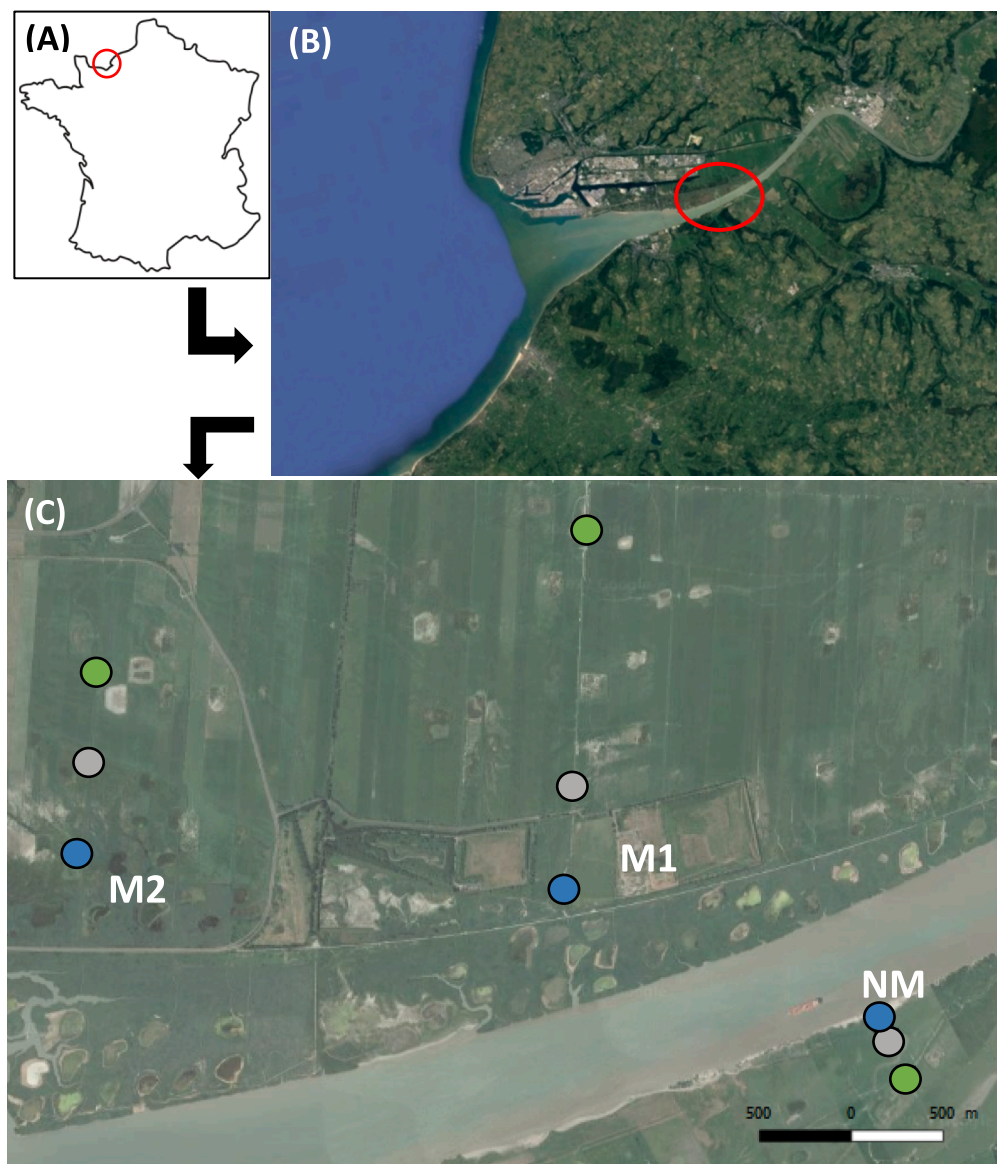


Fig. 1. Location of the Seine estuary in France (A) and global location of the study areas in the Seine estuary (B). Location of the three study sites (C), and location of sampled zones within each study sites (high in green, middle in grey and low in blue). NM = Non Managed site, M1 = Managed site one and M2 = Managed site two. Sampling design applied on each site is illustrated in (D). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

closest to furthest from the sea. On each site, three zones of 50 m² were defined according to their topography: high, middle, and low zones, using a digital elevation model of the Seine estuary (GIP *Seine-Aval*, 2012) (Fig. 1D) and vegetation community characteristics (e.g., the presence of salt-tolerant species like *Bolboschoenus maritimus* and *Juncus gerardi*). High elevation zones are inundated during exceptional events (e.g., spring tides, storm surges), contrasting with the low elevation zones closest to the river, which are regularly exposed to inundations. Additionally, all study sites are influenced by the characteristic winter flooding of the river Seine, creating a seasonal flooding gradient. However, this is mitigated by the hydraulic control of the waters from the river Seine through the valves and channels present on the north shore. In addition, the study sites present different land uses, with the NM site being grazed across all topographical levels. Site M1 is mowed with late season grazing on the high and intermediate elevation zones, while the low zones are grazed all year round. Finally, site M2 is mown across all elevation zones.

2.2. Sampling design

2.2.1. Spider sampling

To sample spiders, we used two pairs of four sampling points on each of the three topographical zones defined previously for a total of 24 sample points per site (Fig. 1D). At each sampling point, 50 aspirations of 2 s with a thermic aspirator were performed on the ground. The extremity of the *g*-vac measures 10 cm in diameter (i.e., 0.39 m² sampled for each point). The content of the sample was immediately stored in 70 % ethanol to avoid intraspecific predation during transport. Spiders were then sorted in the lab and stored in 70 % ethanol, and adults identified down to species level. This sampling design was repeated four times in 2020 in order to obtain the best possible sampling completeness (from 14 to 16/06, from 22 to 24/07, from 24 to 26/08, and from 14 to 16/09).

2.2.2. Vegetation surveys

On the same three zones along the topographical gradients of the three study sites previously defined for spider sampling, vegetation surveys were carried out within two square plots per zone, each containing a grid of 16 squares of 1 m² for a total of 96 sampling points per site. In each square, indices of vegetation cover based on Braun-Blanquet have been assigned to each plant species (attribution of a class coverage coefficient: r,+,1,2,3,4,5 for all the plant species on the sampled surface). These surveys were carried at species level once per site between 27/05 and 02/07/2020, depending on the site. To account for spatial distribution heterogeneity between taxa, the vegetation surveys were pooled (sum of plants covering) to obtain 24 sample points of 4 m² per site (Fig. 1D). The Braun-Blanquet coefficient was converted into the Van Der Maarel coefficient to limit the weight of rare species.

2.2.3. Environmental variables

Litter depth and vegetation cover were measured using the same spatial protocol applied to the vegetation surveys, with one value for each of the 16 squares defined in each plot. The thickness of the litter was measured once between 25 and 26/08/2020 with an accuracy of 0.5 cm. The vegetation cover was visually assessed once in 2020 (between 27/05/2020 and 02/07/2020). At the same time, vegetation height was also measured at 10 points regularly distributed on each of the two plots previously defined per zone for a total of 72 sampling points per site. In addition to these structural variables, pH and conductivity were measured on the superficial part of the soil (between 0 and 15 cm deep) with three measurements per zone, carried out one time between 30/06 and 01/07/2020 (using a Mettler Toledo FiveEasy sensor).

2.3. Functional traits used

In order to assess the functional diversity of plants and spiders (see below for the method), functional traits were assigned to each species following existing literature. The definition of functional trait provided by *Violle et al. (2007)* and followed by *Wong et al. (2019)* was used according to previous work on these taxa as bioindicators (*Hacala et al., 2024*). The traits selected here are seen as broadly comparable between taxa. Respectively for spiders and plants: global development (maximum size of females and maximum height), annual periodicity (seasonal activity; start of flowering periods and vegetative formation), access to resources (hunting strategies; leaf dry matter content (LDMC) and specific leaf area (SLA)), and dispersal ability (ballooning ability; dissemination type). These functional traits are known to be linked to environmental changes in both spiders (*Ridel et al., 2021; Hacala et al., 2024*) and vegetation (*Abgrall et al., 2017*).

For spiders, traits were extracted from the literature: see (*Roberts, 1985; 1987; Uetz, 1999; Harvey, Nellig, & Telfer, 2002; Bell et al., 2005; Cristofoli et al., 2010; Cardoso et al., 2011; Simonneau, Courtial, & Pétilion, 2016*). These traits were then analyzed jointly by using functional diversity analysis (see paragraph below) and not separately, since the objective here is to describe the variation in overall functional diversities across study sites and topographical zones. Missing trait values from literature (particularly for ballooning) were completed by linking them to the closest genus available. The patterns obtained with this method remained similar to those obtained with keeping missing values. Average plant leaf traits were extracted from the TRY database (*Kattge et al., 2020*) and root traits from the Global Root Traits database (GRoOT; *Guerrero-Ramírez et al., 2021*). They were completed with overall life strategies from the baseflor database (*Julve, 2018*). A summary of the modalities of each trait used here is attached in [Appendix 1](#).

2.4. Statistical analyses

2.4.1. Habitat characteristics

In order to highlight whether the environmental variables differed between the three topographical zones of each of the sites, ANOVA tests followed by Tukey post-hoc tests or Kruskal–Wallis followed by Dunn tests were carried out depending on the homoskedasticity and normality of the model's residuals respectively. Holm correction was used for post-hoc tests if necessary. All statistical analyses were performed using R STUDIO software (v. 4.3.2). and packages detailed hereafter.

2.4.2. Taxonomic vs functional diversity patterns and Q order influence

Taxonomic diversity was estimated with the INEXT.3D package (v. 1.0.1) (*Chao et al., 2021*) for each Q diversity order (Q0, Q1, and Q2), corresponding to different weights attributed to rare species. For $q = 0$ the Hill number corresponds to the specific (or functional) richness, with all species have the same weight regardless of their abundance. For $q = 1$, the Hill number corresponds to the exponential of Shannon entropy, with species weighted with respect to their abundance. Finally, for $q = 2$ the Hill number corresponds to the inverse of Simpson index, so the abundant species are favored and rare species are discounted (*Chao et al., 2014*). These indices were calculated for each topographical zone and for each site for both taxa using the iNEXT3D function with 50 bootstrap replicates. This method considers the sample coverage and therefore avoids the risk of false conclusions due to insufficient sampling. For spiders, the individuals present in the different sampling sessions were pooled. Similarly, functional diversity was estimated using the INEXT.3D package for each Q order previously mentioned, defined as being comparable to the calculation method used for taxonomic diversity (for more details on the methods, see *Chao, Chiu, & Jost, 2014; Chao et al., 2021*). This method defines the absence of overlap in the confidence interval of produced curves as a significant difference. To calculate functional diversity patterns for each q order, all functional traits were computed in a species X traits matrix, and confronted to a

species abundance X treatment (here the topographic zones) matrix using Rao’s quadratic entropy Q, which represents the mean functional distance between any two individuals randomly selected from the assemblage. The measure of functional diversity quantifies the effective number of equally distinct functional groups. In the same way than for taxonomic diversity methods, when $q = 0$ functional diversity equals the effective number of functional groups. For $q = 1$ and $q = 2$, functional diversities result from the transformation of Shannon entropy and Rao’s quadratic entropy indices (see Chao et al., 2019 for more details).

2.4.3. Differences in community composition and species richness

To test differences in terms of composition and abundance between sites for each taxon, PERMANOVA was performed with the adonis2 function (vegan package, v.2.6–4) in a Bray-Curtis distance matrix. If tests signaled significant differences, multiple comparison tests were carried out with the pairwise.adonis2 function (pairwiseAdonis package) on the model.

2.4.4. Indicator species

To identify indicator species of each topographic zone per site, the indicator index (IndVal) proposed by Dufrene and Legendre (1997) was calculated using the multipatt function (indicpecies package, v. 1.7.14). According to the described methods, a threshold level of 25 % for the index was considered significant, indicating the presence of the species in more than 50 % of the traps in targeted topographic zones as well as a relative abundance of more than 50 % in this zone.

2.4.5. Proportion of halophilic species

To compare the proportion of halophilic species between topographic zones per site, the halophilic character was attributed to each spider species according to the literature and coded with binary responses (halophilic species vs. non-halophilic species). Vegetation tolerance to salinity was assessed using average Ellenberg indicator values for salt tolerance from the TRY database (Kattge et al., 2020). Afterwards, community-weighted means were calculated with the funtcomp function (FD package, v. 1.0–12.3) on a presence/absence matrix (equal weight for each species) and on an abundance matrix for both taxa (abundance proportional weight). Then, significant differences between topographic zones were assessed by ANOVA tests followed by Tukey post-hoc tests or Kruskal–Wallis followed by Dunn tests with Holm correction where appropriate.

Table 1

Environmental variables (mean ± s.d., n = 8) for each zone and for each site. (Successive letters indicate significant differences. H, high; M, middle; L, low. NM = Non Managed site, M1 = Managed site one and M2 = Managed site two.

		NM			M1			M2					
average height of vegetation (cm)	H	38.6	±	14.5	a	97.0	±	14.7	A	101.0	±	22.7	x
	M	34.4	±	8.5	a	90.6	±	10.4	A	61.6	±	22.9	y
	L	41.3	±	12.2	a	60.8	±	6.1	B	56.6	±	16.2	y
total vegetation cover (%)	H	100.0	±	0.0	a	100.0	±	0.0	A	100.0	±	0.0	xy
	M	99.8	±	0.4	a	100.0	±	0.0	A	100.0	±	0.0	x
	L	82.3	±	10.5	b	100.0	±	0.0	A	99.2	±	2.5	y
litter depth (cm)	H	0.0	±	0.0	a	0.7	±	0.5	A	0.2	±	0.3	x
	M	0.0	±	0.0	a	0.3	±	0.4	B	1.5	±	0.8	y
	L	0.0	±	0.0	a	1.1	±	0.7	C	2.0	±	0.7	z
soil conductivity (µS/cm)	H	524.8	±	101.2	a	1361.7	±	1527.3	A	427.9	±	164.8	x
	M	1010.9	±	212.6	b	1186.3	±	305.3	A	225.6	±	40.0	x
	L	1917.3	±	148.5	c	2531.3	±	618.9	A	744.8	±	365.0	x
pH	H	7.8	±	0.1	a	7.9	±	0.3	A	7.9	±	0.1	x
	M	8.1	±	0.0	b	8.0	±	0.1	A	8.0	±	0.0	x
	L	8.2	±	0.1	b	7.7	±	0.2	A	7.9	±	0.1	x

3. Results

3.1. Habitat characteristics

As expected, the non-managed site NM featured an increase in salinity from the high to the low zones as well as a slightly lower vegetation cover in the low areas (Table 1). The managed site M1 is characterized by a significant increase in the litter depth from the high to the low areas, high global vegetation cover, and similar conductivity measured between each topographic zone. Salinity standard deviation of the high topographic zone appeared particularly strong on this site. Finally, the managed site M2 is characterized by a significant increase in the litter depth and smaller vegetation height in the middle and low zones. Moreover, salinity appeared similar between each topographic zone and surprisingly, the measured values were low.

3.2. Taxonomic vs functional diversities patterns and Q order influence

On the non-managed site NM, species richness of spiders was similar for each topographic zone due to the high variability of estimated values (especially for high and low zones) (Fig. 2A). The Shannon and Simpson diversity indices were found to be highest in the low zones and lowest in the middle and low zones, without a statistically significant difference between the two indices. For plants, a similar pattern was obtained for each Q order, with diversity significantly decreasing from the upper zone to the lower (Fig. 2B). On this site, the functional richness of spiders showed a similar pattern to species richness with no significant difference between each topographic zone (Fig. 3A). Similarly, functional diversity for the other Q orders showed maximal values in the low zones and minimal values for middle and low zones without significant difference. For plants, functional richness appeared significantly higher in the upper zone but similar in middle and low zones. This pattern remained true for each Q order (Fig. 3B).

In managed site M1, spider species richness ($q = 0$) appeared higher in the low zone and similar between the middle and high zones (Fig. 4A). This pattern was also found for the other Q orders. In contrast, the species richness of plants appeared maximal for the high zone, intermediate for the low zone, and minimal for the middle zone (Fig. 4B). Moreover, for this taxon, specific diversity remained at a maximum in the upper zone according to all the Q orders, but the middle zone was respectively lower than the low zone for species richness, equal for Shannon diversity, and higher for Simpson diversity.

Spider functional richness was recorded as similar between each topographic zone, contrasting with species richness (Fig. 5A). For other Q orders, higher values were obtained for the lower zone and similar

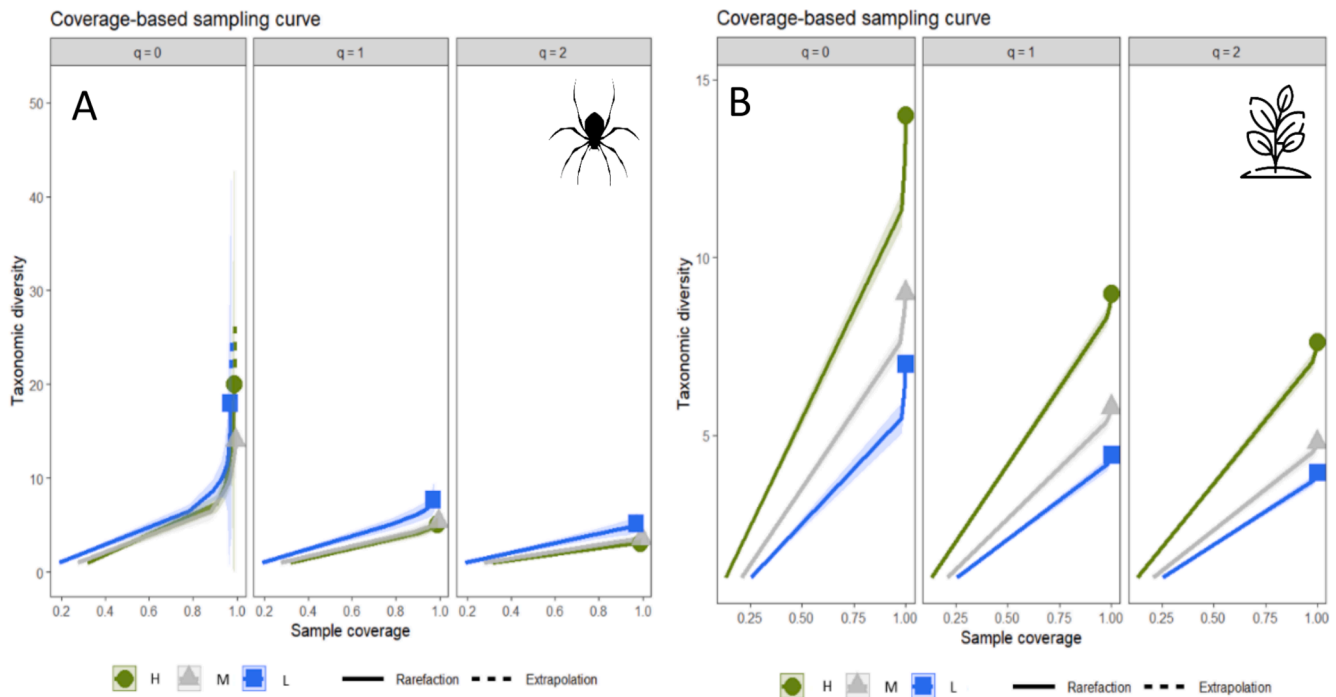


Fig. 2. Rarefaction curves for taxonomic diversity between topographic zones (H = High, M = Middle and L = low) in the Non-Managed site (NM), for each diversity order (Q0, Q1 and Q2), and for each taxa (A, spiders and B plants).

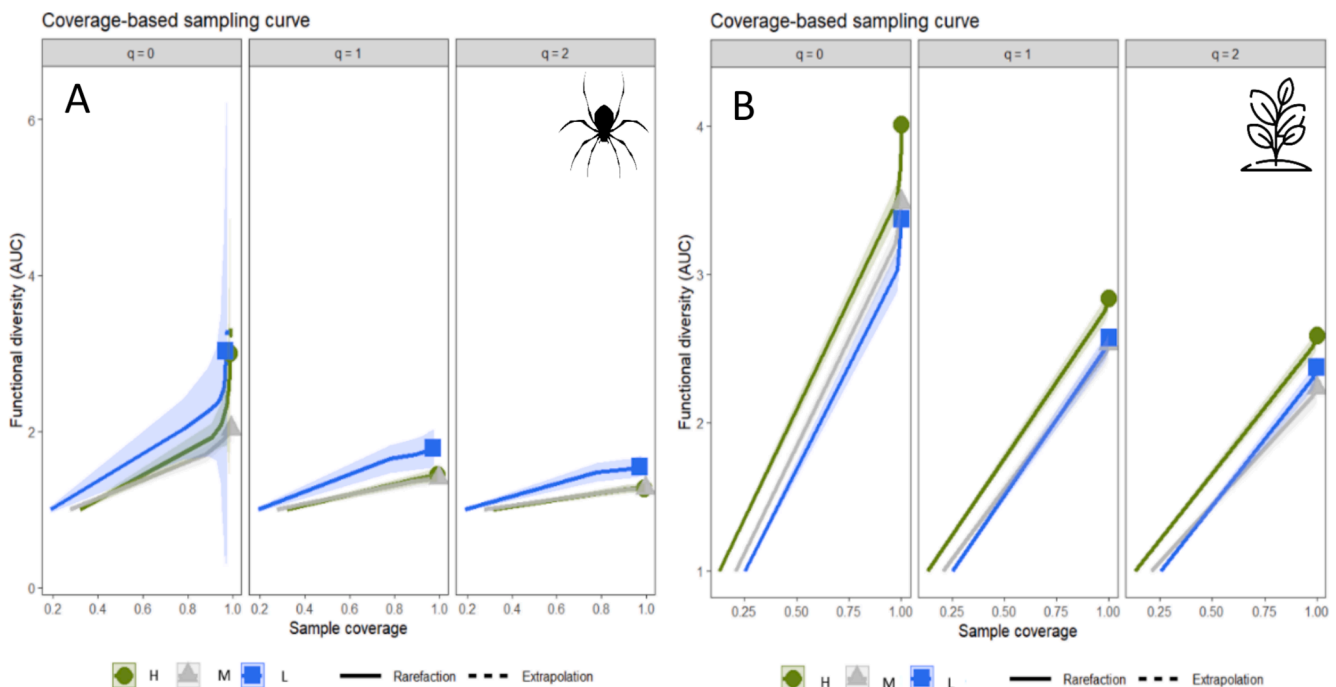


Fig. 3. Rarefaction curves for functional diversity between topographic zones (H = High, M = Middle and L = low) in the Non-Managed site (NM) for each diversity order (Q0, Q1 and Q2), and for each taxa (A, spiders and B plants).

values for high and middle zones, similar to those obtained for taxonomic diversity. For plants, all functional diversity values between Q orders appeared highest for the high elevation zone, intermediate for the low elevation zone, and lowest for the middle elevation zone (Fig. 5B). This pattern is congruent with those obtained for species richness but different from those obtained for Shannon and Simpson diversity.

On managed site M2, spider species richness ($q = 0$) in the high elevation zone appeared higher than in the low elevation zone. The

middle zone displayed intermediate and similar values (Fig. 6A). In contrast, for Shannon diversity ($q = 1$), maximal diversity was still observed in the upper elevation zone while the diversity of the middle and lower elevation zones was lower and similar to one another. Regarding Simpson diversity ($q = 2$), the high and middle elevation zones showed different values but no significant difference was noted between low vs high or middle elevation zones. For plants, a similar pattern was obtained for each diversity Q order with significant

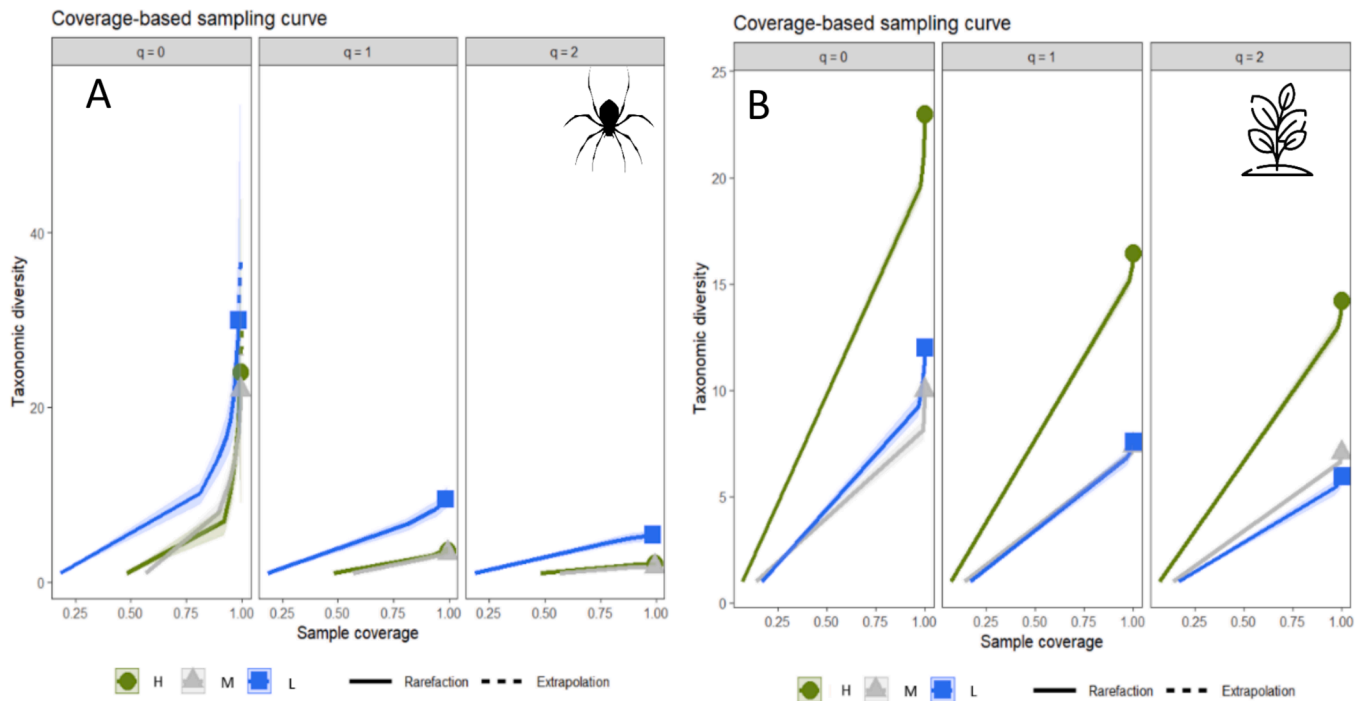


Fig. 4. Rarefaction curves for taxonomic diversity between topographic zones (H = High, M = Middle and L = low) in the managed site one (M1) for each diversity order (Q0, Q1 and Q2), and for each taxa (A, spiders and B plants).

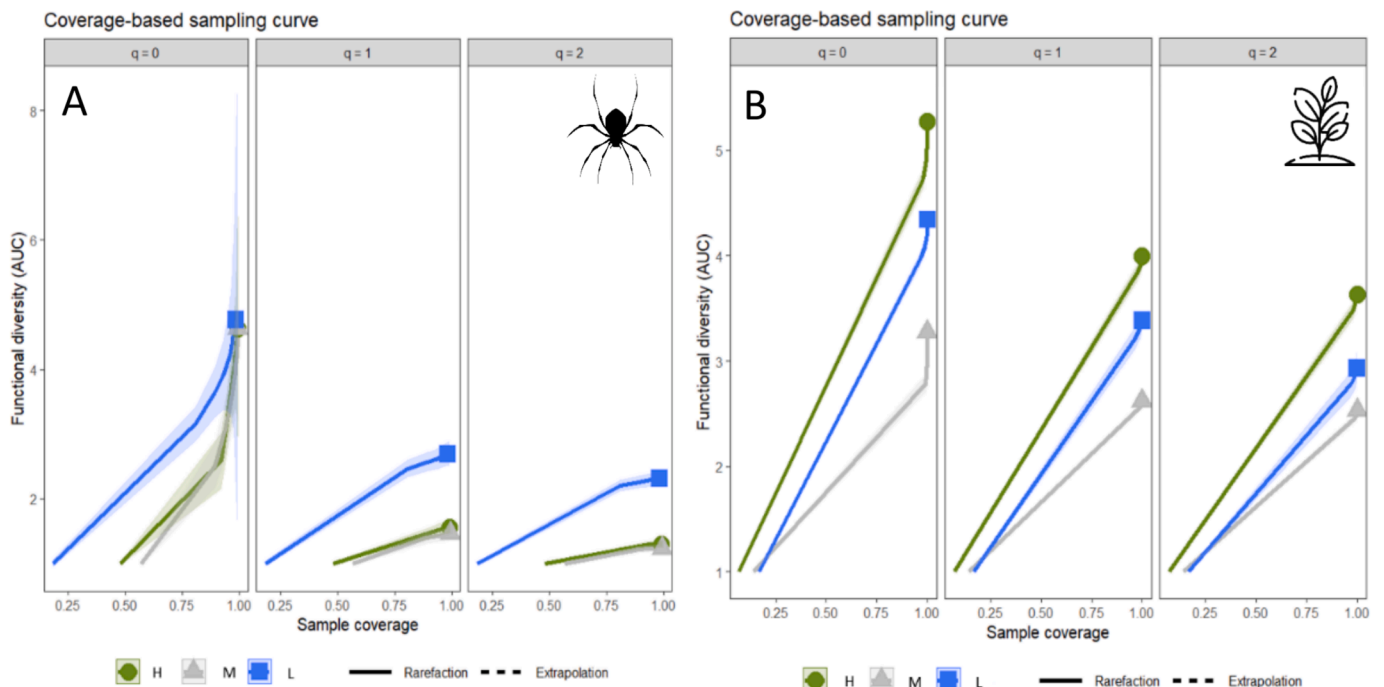


Fig. 5. Rarefaction curves for functional diversity between topographic zones (H = High, M = Middle and L = low) in the managed site one (M1) for each diversity order (Q0, Q1 and Q2), and for each taxa (A, spiders and B, plants).

differences between all topographic zones. The highest value was obtained for the middle zone, intermediate value for the high elevation zone, and minimal value for the low elevation zone (Fig. 6B).

On this site, spider functional richness ($q = 0$) appeared similar for each topographic zone (Fig. 7A). For the other Q orders, the diversity values of the middle elevation zones stood out, being significantly different from the high and low elevation zones. For plants, the global

pattern does not change between diversity Q orders, with the highest value obtained for the middle zone, intermediate value for the high zone, and minimal value for the low zone, consistent with taxonomic diversity (Fig. 7B).

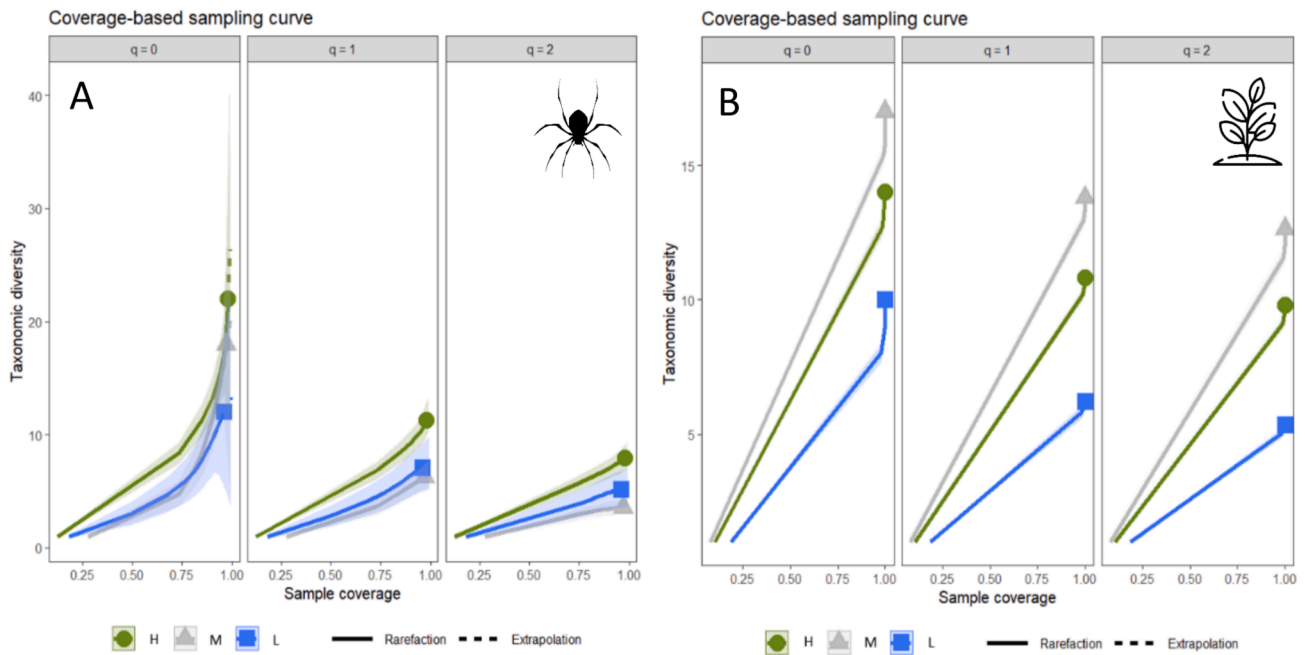


Fig. 6. Rarefaction curves for taxonomic diversity between topographic zones (H = High, M = Middle and L = low) in the managed site two (M2) for each diversity order (Q0, Q1 and Q2), and for each taxa (A, spiders and B plants).

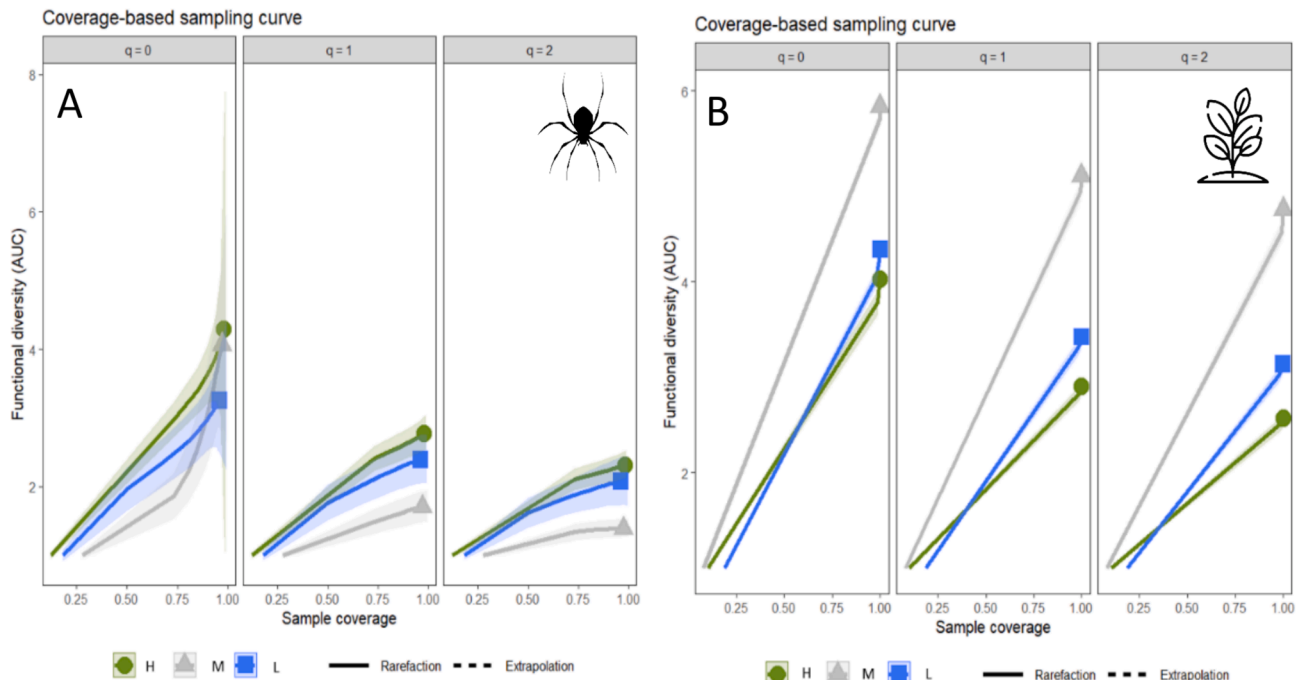


Fig. 7. Rarefaction curves for functional diversity between topographic zones (H = High, M = Middle and L = low) in the managed site two (M2) for each diversity order (Q0, Q1 and Q2), and for each taxa (A, spiders and B, plants).

3.3. Composition

The composition and abundance of both spiders and plants showed significant differences between sites (p-value systematically lower than 0.001; see appendix 2 for more details on test values). More precisely, site by site, all topographic zones appeared significantly different from each other for spider composition (p-value systematically lower than 0.001 except for the managed site M1 high vs middle zones $p = 0.003$). Similarly, all topographic zones appeared significantly different from

each other for plant composition (p-value systematically lower than 0.001 except for managed site M2 high vs middle zones $p = 0.002$) (see appendices 3, 4, and 5 for more details on test values).

3.4. Indicator species

In the non-managed site NM, two spider species appeared as significant indicator species for the high elevation zone (*Agyneta mollis* and *Pachygnatha clercki*), none for the middle zone, and just one (*Pardosa*

purbeckensis) in the low elevation zone (Table 2). For plants, six species (*Hordeum secalinum*; *Phleum pratense*; *Trifolium repens*; *Potentilla anserina*; *Cynosurus cristatus*; *Holcus lanatus*) were identified as significantly indicative for the high zone and none for the middle and low zones (Table 3).

In managed site M1, only one spider species (*Ozyptila sanctuaria*) was noted as significantly indicative for the high elevation zone, none for the middle zone, and four for the low elevation zone (*Pardosa proxima*; *Pardosa prativaga*; *Piratula latitans*; *Arctosa leopardus*). Interestingly, all indicator spider species of the low elevation zone belong to the same family, the Lycosidae. Concerning plants, indicator species showed a different pattern to that obtained for spiders on this site, with a large number of indicator species in the upper elevation zone (11 species, see Table 3 for details), then a single species (*Phleum pratense*) for the middle zone and three species for the lower zone (*Ranunculus sardous*; *Atriplex prostrata*; *Oenanthe fistulosa*).

Concerning managed site M2, a large number of spiders species were recorded as indicators of the upper elevation zone with seven species distributed across three families (see Table 2 for details). For the middle and lower elevation zones of this site, only one spider species, was recorded as an indicator species (respectively: *Gnathonarium dentatum* and *Pirata piraticus*). For plants, an equal number of five indicator species were found for the high and middle zones (respectively: *Bromus racemosus*; *Festuca arundinacea*; *Holcus lanatus*; *Lolium perenne*; *Cynosurus cristatus* and *Juncus articulatus*; *Carex otrubae*; *Juncus gerardii*; *Myosotis laxa*; *Alopecurus geniculatus*), while no species were identified as indicative of the lower zone.

3.5. Salinity affinity

On the non-managed site NM, the proportion of halophilic spider species showed increasing values from the high elevation to the low elevation zone, with significant differences observed among all values obtained for the topographical zones (Fig. 8.A1). Interestingly, when weighted by abundance, only the lower elevation zone appeared to have significantly fewer species compared to the middle and high elevation

Table 2
Significant indicator spider's species foreach topographic zones (H = High, M = Middle and L = low) per study site, and associated p-value. Halophilic species are in bold. NM = Non Managed site, M1 = Managed site one and M2 = Managed site two. Signif. codes: ***: p < 0.001 **: p < 0.01 *: p < 0.05.

	NM		M1		M2	
	species	p	species	p	species	p
H	<i>Agyneta mollis</i>	0.030	<i>Ozyptila sanctuaria</i>	0.015	<i>Agyneta mollis</i>	0.001
	<i>Pachygnatha clercki</i>	0.032			<i>Tenuiphantes tenuis</i>	0.001
					<i>Pardosa proxima</i>	0.001
					<i>Agyneta rurestris</i>	0.001
					<i>Oedothorax retusus</i>	0.013
					<i>Pardosa palustris</i>	0.024
					<i>Enoplognatha mordax</i>	0.009
M	/		/		<i>Gnathonarium dentatum</i>	0.012
L	<i>Pardosa purbeckensis</i>	0.001	<i>Pardosa proxima</i>	0.001	<i>Pirata piraticus</i>	0.003
			<i>Pardosa prativaga</i>	0.001		
			<i>Piratula latitans</i>	0.003		
			<i>Arctosa leopardus</i>	0.018		
				*		

zones, with no significant difference between the latter (Fig. 8.A2). Similarly, for plants, the mean Ellenberg salinity value followed the same pattern as observed for spiders, with significantly increasing values from the high elevation to the low elevation zones (Fig. 8.B1). The results obtained with abundance-weighted values appeared consistent with this pattern (Fig. 8.B2).

On managed site M1, there were no significant differences observed in the proportion of halophilic spider species present in the assemblages among the various topographical zones (Fig. 8.A1). This pattern was also evident for the proportion of halophilic individuals when weighted by species abundance (Fig. 8.A2). However, for plants, the mean Ellenberg salinity value of the assemblage appeared maximal for the high and low elevation zones, with no significant difference between them, while significantly fewer halophytes were found in the middle zone (Fig. 8.B1). A similar pattern was observed for the abundance-weighted metric (CWM) (Fig. 8.B2).

On managed site M2, the proportion of halophilic spider species appeared to be higher in the high elevation zone, lower in the low elevation zones, and intermediate but not significantly different from each other in the middle zone (Fig. 8.A1). This pattern remained consistent when abundance-weighted metrics were considered (Fig. 8.A2). For plants, the mean Ellenberg salinity value showed significantly higher values for the middle zone compared to the others, with similar values observed between the high and low elevation zones (Fig. 8.B1). However, when abundance-weighted values were considered, the middle zone still appeared significantly higher, with the high elevation zone showing an intermediate value and the low elevation zone showing a significantly lower value compared to the upper zone (Fig. 8.B2).

4. Discussion

4.1. Habitat characteristics

For the non-managed site NM, the observed salinity gradient corresponds to the rhythm of tidal flooding. The lower vegetation cover in the low topographical zones may be a consequence of grazing on wetlands, as livestock has been shown to increase the frequency and duration of waterlogging through trampling and soil compaction (Dausse et al. 2012). It could be due to the sediment dynamics deposition during tidal flooding, which can limit plant extension (Langlois et al, 2003). In managed site M1, the significant increase in litter depth could be attributed to the water management practices. During the winter period, water valves are closed (Reserve Naturelle Estuaire de Seine 2023), leading to water retention and consequently accumulation of litter that cannot be discharged into the Seine River. The similarity of salinity levels across each topographic zone in this site corresponds to the water management practices. Moreover, the variability in salinity measurements in the high elevation zones could be attributed to dredging activity in this area, resulting in soil with heterogeneous properties, as supported by the high variability in granulometry measured in another research work (Neupert et al., 2024).

Furthermore, the higher litter depth observed in the lower topographic zone of managed site M2 aligns with the previous observation of water retention during winter, and the uniformity of salinity throughout the site is consistent with water level management. However, the low soil salinity values measured on this site were unexpected given its proximity to the river mouth, and could be indicative of a hydrological anomaly, possibly linked to the upwelling of freshwater from the karst aquifers of the surrounding chalk cliffs, as suggested by Neupert et al. (2024) and Soueid-Ahmed et al. (2017).

4.2. Taxonomic vs functional diversity patterns

For the non-managed site NM, a contrasting pattern was observed between the taxonomic diversity of spiders and plants, supporting our initial hypothesis of high complementarity between indicator taxa

Table 3

Significant indicator plants species for each topographic zone (H = High, M = Middle and L = low) per study site, and associated p-value. Ellenberg salinity value are reported for each species. NM = Non Managed site, M1 = Managed site one and M2 = Managed site two. Signif. codes: ***: $p < 0.001$ **: $p < 0.01$ *: $p < 0.05$.

NM			M1			M2		
Species	p	Ellenberg salinity	Species	p	Ellenberg salinity	Species	p	Ellenberg salinity
H								
<i>Hordeum secalinum</i>	0.001***	2.00	<i>Arrhenatherum elatius</i>	0.001***	0.50	<i>Bromus racemosus</i>	0.001***	0.50
<i>Phleum pratense</i>	0.001***	0.33	<i>Holcus lanatus</i>	0.001***	0.67	<i>Festuca arundinacea</i>	0.001***	1.83
<i>Trifolium repens</i>	0.003**	1.25	<i>Plantago lanceolata</i>	0.001***	0.50	<i>Holcus lanatus</i>	0.001***	0.67
<i>Potentilla anserina</i>	0.001***	2.25	<i>Potentilla anserina</i>	0.001***	2.25	<i>Lolium perenne</i>	0.001***	0.33
<i>Cynosurus cristatus</i>	0.006**	0.00	<i>Carex distans</i>	0.001***	4.00	<i>Cynosurus cristatus</i>	0.001***	0.00
<i>Holcus lanatus</i>	0.019*	0.67	<i>Trifolium pratense</i>	0.001***	0.60			
			<i>Plantago major</i>	0.002**	0.60			
			<i>Juncus gerardii</i>	0.007**	6.00			
			<i>Crepis biennis</i>	0.008**	0.33			
			<i>Cynosurus cristatus</i>	0.014*	0.00			
			<i>Lotus corniculatus</i>	0.017*	0.75			
M	/		<i>Phleum pratense</i>	0.001***	0.33	<i>Juncus articulatus</i>	0.001***	1.00
						<i>Carex otrubae</i>	0.001***	2.00
						<i>Juncus gerardii</i>	0.001***	6.00
						<i>Myosotis laxa</i>	0.008**	0.00
						<i>Alopecurus geniculatus</i>	0.004**	1.25
L	/		<i>Ranunculus sardous</i>	0.001***	2.20	/		
			<i>Atriplex prostrata</i>	0.001***	1.80			
			<i>Oenanthe fistulosa</i>	0.002**	0.33			

(Lafage et al., 2015; Hacala et al., 2020; Hacala et al., 2024). Specifically, while a similar pattern was observed for spider species richness across topographical levels, decreasing richness values were obtained for plants with decreasing elevation, typically indicative of a stress gradient (i.e., reduction in species richness due to increasing abiotic filter strengths). This result could reflect a turnover process in spider assemblages without influencing taxonomic richness, possibly due to insufficient salinity to filter only halophilic species, as observed in harsher environments like salt marshes (Pétillon et al., 2003). These results suggest a weaker specific selection on spider species compared to plant species on this site, possibly due to their higher mobility compared to sessile organisms (Lafage et al., 2015). The pattern of spider functional richness, similar to species richness, is consistent with the high correlation between these two metrics (Pavoine et al., 2013), supporting species selection based on functional characteristics, as previously observed for spiders in harsher environments (Ridel et al., 2021). Conversely, the similar functional richness of plants in the middle and low elevation zones, contrasting with previous results, suggests functional trait convergence among present species (Meinzer, 2003).

In managed site M1, the complementarity of spider versus plant taxonomic diversity was also evident. Specifically, the higher spider species richness observed in the lower zone could be linked to the increased litter depth, resulting from limited discharge of organic matter into the Seine River, which may enhance spider species diversity by reducing interspecific competition (Döbel et al., 1990). Conversely, the highest species richness was recorded in the high elevation zones, possibly due to the high salinity variability, suggesting co-occurrence of species with different ecological affinities by reducing interspecific competition (Crain et al., 2004). This heterogeneity could be linked to dredging activity, as previously mentioned. Contrasting patterns were also noted in functional diversity between plants and spiders, highlighting their complementary functional roles, according to other study (Hacala et al., 2024). Interestingly, spider functional richness showed no difference between topographic zones, contrasting with taxonomic richness results, suggesting a diversification of species that are functionally similar, possibly linked to similar environmental structures driving spider functional assemblages (Leroy et al., 2014). Conversely, for plants, the pattern obtained for functional richness aligned with

previous results, supporting a global redundancy between these metrics for this taxon (Pavoine et al., 2013).

Managed site M2 remained consistent with other study sites regarding the observed complementarity between taxa. Specifically, the reduction in spider species richness from high to low topographic zones is consistent with environmental filtering processes (Pétillon et al., 2008). This result contrasts with the water level management of this site by valves but could be linked to freshwater resurgence (i.e., upwelling of freshwater from karst aquifers), as spider assemblages are sensitive to flooding and/or hydric soil conditions (Fournier et al., 2015). Conversely, plant species richness appeared higher in the middle zone, possibly linked to freshwater upwelling coupled with restrictions on tidal influence, generating intermediate environmental conditions allowing the co-occurrence of different species types (i.e., halophilic and hygrophilous species). In terms of functionality, the spider pattern remained generally coherent with the taxonomic one, with minor differences observed between pairs of topographical zones but no shifting patterns (Pavoine et al., 2013; Ridet et al., 2021). In contrast to this result, plant diversity in the lower zone appeared to shift from lower taxonomic to intermediate functional richness values. This result could be linked to the partial selection of flooding specialist species in the lower zone, reducing taxonomic but increasing functional diversity due to high divergence between functional hygrophilous and salt-tolerant species.

4.3. Q order influence

As expected, on the non-managed site NM, the patterns of taxonomic and functional diversity of spiders changed between Q orders. Surprisingly, for abundance-weighted metrics, diversity in the low elevation zone appeared higher. This suggests balanced proportions of halophilic and non-halophilic species near the Seine River, possibly due to an increasing proportion of specialist species in this zone. This supports lightly filtered spider assemblages (i.e. no exclusion of generalist species) compared to harsher environments (Pétillon et al., 2008; Ridet et al., 2021), which is consistent with the site's position furthest from the sea on the lateral gradient. For plants, taxonomic and functional diversity patterns did not significantly change with Q order on this site,

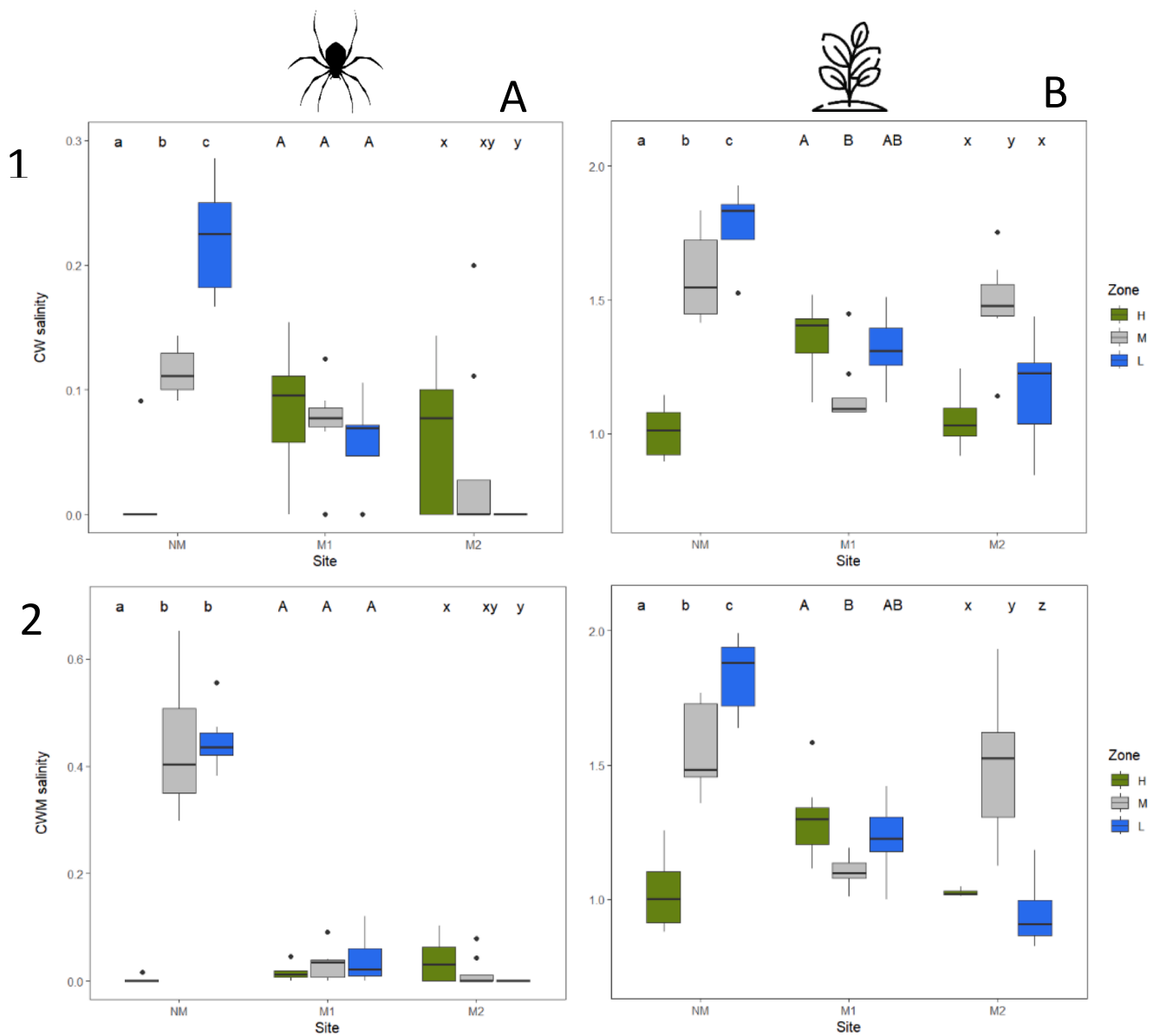


Fig. 8. Boxplot on spiders’ (A) and plants (B) community weighted traits for salinity affinity (for species, 1 and for individuals, 2) for each site and for each topographic zone (H = High, M = Middle and L = low). Salinity affinity is halophilic species or not for spiders, and Ellenberg salinity value for plants. (Successive letters indicate significant differences by ANOVA test followed by Tukey post-hoc tests or Kruskal–Wallis followed by Dunn tests, where appropriate. Holm correction was used for post-hoc tests if necessary). NM = Non-Managed site, M1 = Managed site one and M2 = Managed site two.

suggesting a high turnover process (Yuan et al., 2012). This interesting contrast between spiders and plants highlights different spatial responses to environmental filtering.

On managed site M1, the patterns observed for spider diversity remain consistent for each Q order, in line with the initial hypothesis (Hacala et al., 2024). In contrast, functional patterns for spiders diverge from this previous stability, supporting the hypothesis of functional convergence mentioned above. However, for plants, the shifting of taxonomic diversity values between middle and low elevation zones as Q order increases supports unbalanced abundance in the lower zones, possibly due to winter flooding in that area (Fournier et al., 2015). On the other hand, functional plant diversity remains stable between each Q order, suggesting functional redundancy between some rare and abundant species (Meinzer, 2003).

On managed site M2, the shifting position of spider taxonomic and functional diversity in the middle zone indicates unbalanced abundance. In this site, the upwelling of freshwater from the water table creates

longer periods of waterlogging and reduced soil salinity, which could favor the presence of hygrophilous species. Conversely, taxonomic and functional patterns of plants remain stable between Q orders, suggesting a higher influence of environmental filtering on composition than on abundance for this taxon at the spatial scale of the defined topographical gradient. Interestingly, a general taxonomic and functional convergence was observed for spiders on this site, coupled with an effect of Q order on functional metrics, contrasting with the taxonomic and functional divergence observed for plants, with an effect of Q order on taxonomic metrics. This underscores the strong complementarity between the bioindicator taxa used (Lafage et al., 2015; Hacala et al., 2020; 2024).

4.4. Composition of assemblages

According to our initial hypothesis, there are differences in the specific composition and abundance between sites, indicating the sensitivity of spiders and plants to water management types (non-

managed vs managed), consistent with their sensitivity to flooding and salinity (respectively Pétilion et al., 2003; Pétilion et al., 2014; Fournier et al., 2015; Ridel et al., 2021, and McKee & Mendelssohn, 1989; Reed, 1995; Gough & Grace, 1998; Flindt et al., 1999). However, differences in composition between managed sites highlight the sensitivity of these taxa to local parameters and exploitation types (mowing and grazing). Site by site, the differences in composition partially contrast with the results on diversity (e.g., different composition but similar diversity obtained in spider taxonomic diversity between high and middle elevation zones on managed site M1). This opposition can indicate shifting assemblages, sometimes based on composition rather than on species proportion, highlighting high turnover, as observed in other coastal systems (see for spiders: Pétilion et al., 2008; Coccia & Farina, 2019 and for plants: Janousek & Folger, 2014; Lawrence et al., 2022).

4.5. Indicator species

On the non-managed site NM, the two spiders indicator species of the high elevation zone (*Agyneta mollis* and *Pachygnatha clercki*) were common and generalist species (Hänggi et al., 1995), indicating low-filtered zones. For the lower elevation zones, the presence of *Pardosa purbeckensis*, a species occurring in shores (Puzin et al., 2014), is consistent with the management type and environmental salinity gradient measured here. For plants, the presence of sub-hydrophilic species indicators of high elevation zones (e.g., *Hordeum secalinum*, *Potentilla anserina*) with the absence of strict halophilic species aligns with the results obtained for spiders.

On managed site M1, the only spider indicator species found for high elevation zone assemblages, *Ozyptila sanctuaria*, is typically found in open habitats (Dawson et al., in prep), consistent with the management type (i.e., mowing with late-season grazing). In the lower elevation zones, the presence of four Lycosidae species supports the diversification of functionally close species linked to an increase in litter depth by adding new prey guilds, favoring ground-hunting species (Döbel et al., 1990; Uetz, 1991). Finally, the presence of *Pirata piraticus* indicates wet conditions in this zone (Harvey et al., 2002). For plants, assemblages show numerous indicator species of high zones, with sub-halophilic species (e.g., *Juncus gerardi*) mixed with non-halophilic species (e.g., *Trifolium pratense*) (Julve, 1998). This co-occurrence of species with different life strategies is congruent with the high taxonomic and functional diversity previously obtained, supporting the strong heterogeneity of this zone. In the lower elevation zone, the three species found (i.e., *Ranunculus sardous*, *Atriplex prostrata*, and *Oenanthe fistulosa*) are hydrophilic species typical of flooded meadows (Julve, 1998), consistent with the wet conditions mentioned above.

Finally, for managed site M2, spiders indicator species in higher zones are principally generalist species, except *Enoplognatha mordax*, a coastal shore species. However, caution is necessary regarding the presence of this halophilic species alone, as it is sometimes found in very different habitats such as agroecosystems (Djoudi et al., 2018), and it is possible that *E. mordax* forms a specific complex (Bosmans & Van Keer, 1999) encompassing strictly halophilic and non-halophilic forms. For middle and low zones, the presence of *Gnathonarium dentatum* and *Pirata piraticus*, two species occurring in flooded habitats (Harvey et al., 2002), supports a high hydric stress gradient, as previously discussed (i.e., freshwater resurgence from the water table). For plants, only mesophilic meadow-characteristic plants were found in the high elevation zones (e.g., *Holcus lanatus*, *Lolium perenne*) (Julve, 1998), illustrating their low environmental constraint. However, in the middle elevation zone, the mixture of hydrophilous plant species (e.g., *Carex otrubae*) (Julve, 1998) and halophilic plants like *Juncus gerardi* contrasts with the absence of halophilic spider species, highlighting the higher sensitivity of this taxa, as previously observed. Moreover, this co-occurrence of different species types (i.e., halophilic and hydrophilous) is consistent with the higher taxonomic and functional diversity previously obtained.

Overall, the absence of indicator species from some topographical

zones for each taxa is due to the absence of some exclusive species, indicating transitional assemblages, as suggested by the presence of indicative species of pooled zones (Appendix 6 and 7).

4.6. Proportion of halophilic species

For spiders, the results obtained are generally consistent with expected patterns, with constant proportions of halophilic species on each managed site and an increasing proportion in the non-managed site NM. An exception should be noted for managed site M2, with higher rates of halophilic species and individuals in the high topographic zones. This result is exclusively linked to the presence of *E. mordax*, listed as a halophilic species. As suggested above, this could be a non-halophilic form of this species here. Further work is needed on this genus given the contrasting ecologies and distributions described for this species (Bosmans & Van Keer, 1999). As expected, when metrics are abundance-weighted, the pattern changed only on the non-managed site NM. However, the results obtained reflect a specific composition with more specialist species in lower elevation zones (Pétilion et al., 2008), but with an equal proportion of specialist individuals, corresponding to lightly filtered spider assemblages without the exclusion of generalist species.

Similarly to spiders, the salinity tolerance index for plants (Ellenberg indicator values) increases near the river Seine on the non-managed site NM, but significant variations were also found on the two managed sites. This more precise response of plants in terms of halophilic species proportion confirms the idea of a generally higher sensitivity to salinity and flooding than spiders. However, this result could be due to the still limited knowledge of spider traits (Pekár et al., 2021), allowing for a qualitative implementation of halophilic affinity for this taxon. Additionally, and contrasting with spiders, the plant salinity tolerance index is broadly consistent with taxonomic and functional diversity values, supporting high heterogeneity and co-occurrence of different species types in some places (e.g., high elevation zone of managed site M1 and middle elevation zone of managed site M2).

5. Conclusion

In conclusion, on the unmanaged site NM, spider assemblages appeared lightly influenced by salinity, exhibiting a turnover of species along the stress gradient and balanced abundance between halophilic and non-halophilic species. Conversely, plant assemblages appeared more strongly influenced by filtering processes, with species selection and functional homogenization from the middle elevation zone towards the river Seine. On managed site M1, spiders seemed to be influenced by local factors, leading to species diversification but functional convergence in the lower elevation zone. The flooding constraints present on this site appeared insufficient to strongly influence these taxa, as evidenced by the unbalanced taxonomic abundance. In contrast, plants appeared more sensitive, exhibiting the co-occurrence of different ecotypes possibly linked with winter flooding, along with functional homogenization in the lower elevation zone indicating stronger environmental filtering. Finally, on managed site M2, resurgence from the water table impacted spider assemblages, showing a response to flooding. Conversely, plants exhibited mixed halophilic and hydrophilous assemblages on this site, illustrating the vegetation's higher sensitivity to low salinity levels.

CRedit authorship contribution statement

Aurélien Ridel: Writing – original draft, Formal analysis. **Markus Neupert:** Writing – review & editing, Validation, Investigation. **Althéa Cadro:** Data curation. **Julio Pedraza:** Formal analysis. **Michael Aubert:** Writing – review & editing. **Estelle Langlois:** Writing – review & editing, Funding acquisition. **Julien Pétilion:** Writing – review & editing, Validation, Supervision, Methodology, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2024.112957>.

Data availability

Data will be made available on request.

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