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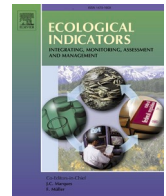
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## Original Articles

# Spider and vascular plant assemblages in subarctic peat bogs are complementary ecological indicators of variation in local and landscape factors

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## ABSTRACT

Despite their specific biodiversity and the ecosystem services they furnish, peat bogs remain poorly understood, especially in terms of their responses to changes at multiple spatial scales. Many subarctic peat systems face acute risks, due to current global change. In this study, using a multi-metric approach, we assessed the relative value of plants and spiders as ecological indicators in contrasted peat bogs of a French archipelago (St. Pierre-et-Miquelon), located in the North Atlantic. In 2021, pitfall trapping and suction sampling collected spiders while phytosociological relevés were used to document vascular plants. A total of 69 species of spiders and 38 species of vascular plants were identified, and both taxonomic (TD) and functional (FD, based on traits related to dispersal, size and ecosystem functioning) diversity were then estimated for three levels of species relative abundance (Hill numbers  $q = 0, 1$  and  $2$ ) using the iNEXT 3D package for alpha diversity as well as iNEXT beta3D for beta diversity. As expected, patterns of TD and FD were highly correlated for each Hill number, but also between Hill numbers for spiders, indicating a surprisingly low effect of species abundance on (spider) diversity patterns. On the contrary, differences between sites were more visible for plants species when species coverage was considered ( $q = 1$  and  $q = 2$ ), for both TD and FD, and for alpha and beta diversity. RLQ and Fourth corner analyses indicated differences based on functional traits between sites which were significantly associated with relationships between dispersal modes and mostly local factors for plant assemblages. Finally, variance partitioning on assemblage composition showed the importance of an interaction between local and landscape factors for both plants and spiders, with a relatively high importance of local factors alone for plants. Our study thus revealed the high complementarity of spider vs. plant assemblage-based metrics as indicators of changing local conditions in peat bogs, confirming these both experience rapid change in subarctic climates.

## 1. Introduction

Peat bogs are amongst the most unusual (Minayeva and Sirin, 2012) and endangered habitats on the planet (Pinceloup et al., 2020), covering 4 million of  $\text{km}^2$  across the globe (Rydin et al., 2013). While their important functions within ecosystems are largely accepted within the scientific literature (Bonn et al., 2016), these humid habitats currently suffer the dual threats of destruction from encroaching agriculture and urbanization. Different types of peat bogs are generally classified within a gradient of available nutrients linked to their hydrology (Rydin et al.,

2013). The habitats studied here are bogs (*sensu* Rydin et al., 2013), or more specifically, they are ombrotrophic peat bogs which draw their ecological specificities from their harsh environmental conditions. They are characterized by saturated hydrology, high acidity and a scarcity of nutrients (Rydin et al., 2013). These conditions lead to important levels of specialization in the biodiversity they host (Minayeva and Sirin, 2012), enhancing both their conservation value (Scott et al., 2006a,b) and the interpretive challenges they represent (Räsänen et al., 2023). Bogs of the North American Atlantic coast are unique habitats characterized by a combination of species considered specialist species

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exclusive to poor bog plants and few minerotrophic ones (Damman and Dowhan, 1981; Wells, 1996).

These types of conditions have been previously studied and even if variations in landscape were highlighted as key driving factors (Andersen et al., 2011), the scale and environmental cues present in the published literature are often too localized (a local variable within a given landscape, e.g., Andersen et al., 2011) or too large - at the continental scale (climatic perspectives, e.g. Robroek et al., 2017) to properly understand the dynamics of peat bogs. In addition, peat bog diversities are often studied by simply comparing different types of peat bogs (Payette and Rochefort, 2001) instead of assessing the variation within a single type of peat bog.

There is therefore a need to improve the knowledge of these habitats and their diversity. Ecological indicators may be used as a tool to efficiently assess habitat ecology (McGeoch, 1998) and to inform about specific indicators themselves (Van Straalen and Krivolutsky, 1996), however, as previously stated, it is better to use multiple taxa to assess habitat complexity as different taxa may have diverged ecological sensitivities, potentially revealing complementary responses (Samways et al., 2010; Fattorini et al., 2011).

Amongst the ecological indicators to be documented, spiders were selected, as they are a highly diverse taxon with more than 50,000 known species worldwide (NMBE, 2023). They have a broad enough ecology to have colonized most terrestrial ecological niches on the planet (Foelix, 2011) and they fit the requirement of a good indicator species (McGeoch, 1998; Gerlach et al., 2013) due to their abundance, diversity, ease of sampling, identifiability, and numerous specialized species. In addition, spiders are amongst the taxa with the highest number and ratio of specialized animal species in Canadian peat bogs (Payette & Rochefort, 2001; Spitzer and Danks, 2006), leading to their successful use as indicator taxa (Scott et al., 2006a,b; Buchholz, 2016). The second taxon considered are vascular plants, the most commonly used indicator of ecological variations in peat bogs (e.g., Kuiper et al., 2014; Robroek et al., 2015) and often one of the primary means, after hydrology, of distinguishing different types of peat bogs (Rydin et al., 2013). The combined use of spiders and vegetation is based on their known complementarity when faced with different ecological processes (Pétillon et al., 2014; Hacala et al., 2020). As spiders are almost exclusively predators, their responses are often uncorrelated with the diversity of local vegetation (Lafage et al., 2019) and their sensitivity to landscape features differs largely across vegetation types, including in wetlands (Lafage et al., 2015). The two taxa thus display different responses to ecological cues and variable degrees of correlation between diversity metrics, and their ecological indicator values can be expected to differ globally across spatial scales.

The use of multiple diversity metrics will better serve conservation of peat bog as those metrics are complementary (Tucker et al., 2018; Hacala et al., 2021; Robuchon et al., 2021; Morel et al., 2022) while also contributing to the overall understanding of habitat biodiversity and conservation values (see Webb et al., 2002 in recent literature). The combined use of multiple metrics is found in the recent literature (for arthropods but also more commonly with vegetation: Hacala et al., 2021) and appears essential for a holistic understanding of habitats (Devictor et al., 2010). For instance, the combined usage of taxonomic and functional diversities demonstrate their complementarity as ecological metrics (Leroy et al., 2014; Campbell et al., 2010; Wong et al., 2019; Ridel et al., 2021). As for the order of diversity based on Hill numbers (sensu Chao et al., 2014), they allow for the understanding of the weight of rare and dominant species within an assemblage that could not be properly assessed solely with diversity indices (Schwartz et al., 2000; Gaston and Fuller, 2008; Jain et al., 2014). Finally, the complementarity of alpha and beta diversities allows for the assessment of an assemblage's composition and serves to untangle environmental sensitivities (Socolar et al., 2016). Within peat bogs, the complementarity of multi-metric approaches has highlighted distinct patterns of biodiversity, which can be observed between taxonomic and functional diversity

with vegetation (Robroek et al., 2017) and entomological (Diptera) communities (Taillefer and Wheeler, 2018), between alpha and beta diversity with vegetation (Fontaine et al., 2007) and within diversity orders with spiders (Scott et al., 2006a,b). To the best of our knowledge, these diversity components are complementary, yet have never been used on a single project.

This study aims to understand the complementarity of contrasted taxa and several metrics as ecological indicators of local and landscapes features within peat bogs. As previously stated, this approach has not been previously undertaken in the study of subarctic Atlantic bogs, an often-overlooked habitat (Sikes and Callegari, 2020). For example, arthropod diversity knowledge can vary by 20-fold from subarctic to temperate regions (DeWaard et al., 2019), indicating the need for specialized studies. These knowledge gaps within the subarctic region have been highlighted specifically for Canadian subarctic peat lands (Warner and Asada, 2006). This state of knowledge combined with the current global changes affecting these habitats at a higher rate (Elmqvist et al., 2004; Limpens et al., 2021) stresses the need to improve our knowledge of them.

We hypothesize (1) a high complementarity between taxa as they are known to display different responses to environmental variables (Hacala et al., 2020; Pétillon et al., 2014) and spatial scales (Lafage et al., 2015); (2) a redundancy in taxonomic and functional diversity as the two metrics are generally highly correlated (Pavoine et al., 2013; Hacala et al., 2021), notably in the case of vegetation (Cadotte et al., 2013); (3) that diversity orders will display complementarity by untangling the effects of stressful environments which tend to drive dominance patterns (Perner and Malt, 2003); and (4) that studying alpha and beta diversities will reinforce the complementarity of both taxa as ecological indicators (for both taxonomic and functional diversity), as reported from other habitats (e.g., Lafage et al., 2015; Hacala et al., 2020).

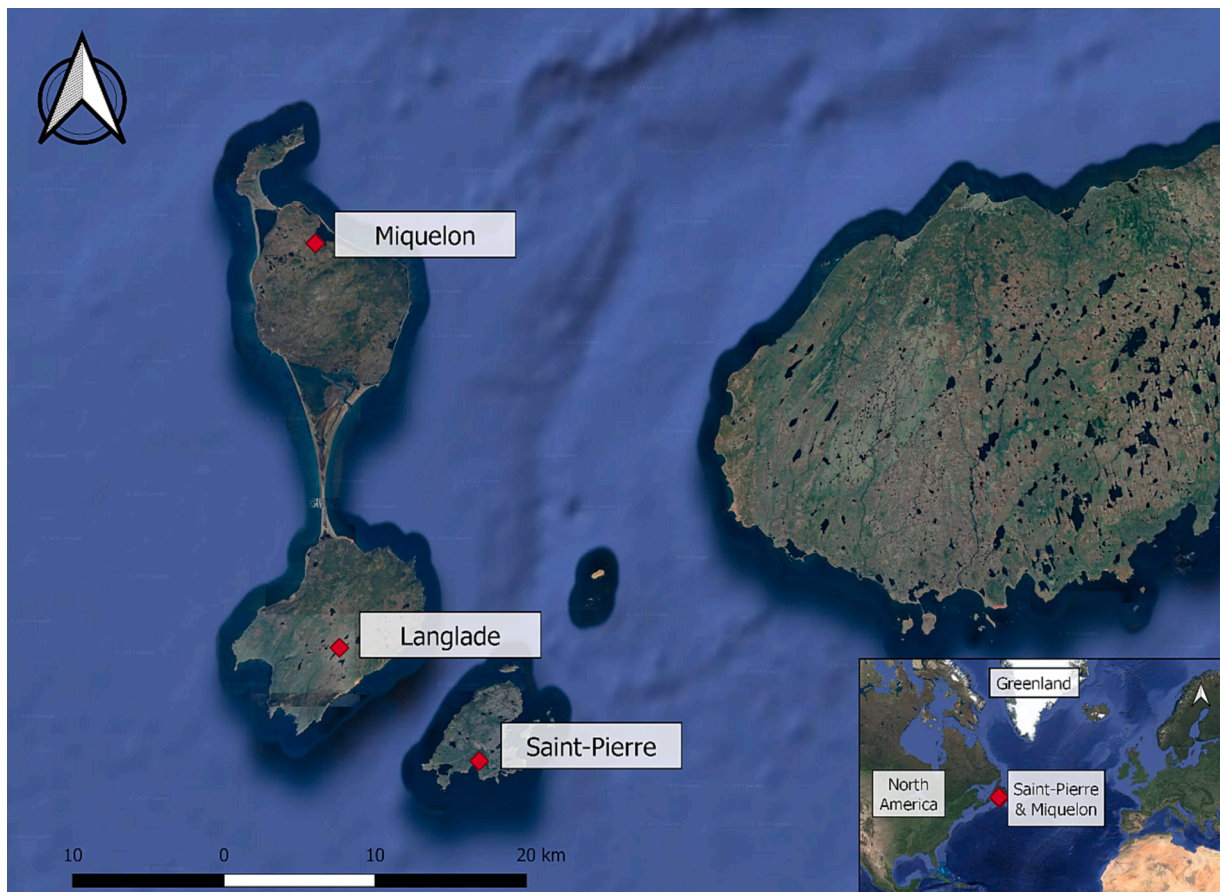
## 2. Material and methods

### 2.1. Study sites

Peat bogs were sampled on three sites on the archipelago of St. Pierre and Miquelon (Fig. 1): St.-Pierre (46.7696 E, -56.1862 N), Miquelon (47.0729, -56.3329) and Langlade (46.8258, -56.3093). These were selected to represent a spectrum of comparable ombrotrophic bogs within contrasted landscape contexts. All three sites were subdivided into three sub-sites of comparable peat bog habitats. St. t. Pierre is characterized by a landscape context composed of anthropogenic areas as well as forest and subarctic heathlands, while the Langlade and Miquelon sites are characterized by large areas of peatland and open water habitats. These two sites resemble each other in terms of landscape composition but they vary in terms of local structure and landscape organization (e.g. the distance between landscape elements and sampling points are greater within Miquelon). The mean temperature of the archipelago is 5.5 °C, with a maximum in August of 15.7 °C and a January minimum of -2.97 °C (mean values calculated from 1933 to 1987, Muller et al., 2012).

### 2.2. Arthropod sampling and vascular plant characterization

In 2021, eight pitfall traps (110 mm in diameter and 150 mm deep) were set on each of the sub-sites for a total of 72 traps. Each trap was associated with a botanical relevé within a square meter where a percentage cover of each plant species was visually estimated. Spatially, groups of four traps were set at least 10 m apart to avoid edge effect and pseudoreplication (Topping and Sunderland, 1992). Each group of four traps formed a sampling point and each trap was set within a five-meter radius of a homogeneous habitat based on dominant vegetation. These were half-filled with a saltwater solution (250 g. L<sup>-1</sup>). A drop of odorless dish soap was added in order to break the surface tension and improve arthropod capture. The contents were collected every two weeks from



**Fig. 1.** Map of St. Pierre & Miquelon. The red dots indicate the three study sites. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

mid-July to the end of August 2021.

Sampling with a suction sampler was performed every two weeks, resulting in four capture sessions, using an inverted leaf blower (15 cm tube diameter, 720 m<sup>3</sup>/h suction capacity). Sampling consisted of 50 times two seconds randomly distributed aspirations across a 20 m side square corresponding to the area sampled by each group of 4 pitfall traps. This resulted in 72 aspiration samples. For the analysis, spiders from the four pitfall traps and the associated suction samples were pooled together as well as the vascular plants data from the four associated relevés.

### 2.3. Identification

Spider samples were sorted in the laboratory, transferred to ethanol 70 %, and stored at the University of Rennes, France. Identification to species level was undertaken using Paquin and Dupérré (2003) on adult spiders, while vascular plant identification was done in the field using Marie-Victorin (1995).

### 2.4. Environmental variables

Environmental variables were assessed at two scales, that of local and landscape. Local variables were air temperature and hygrometry and were measured every 10 min via field data logger (©Tinytag Plus 2 - TGP-4017) during the 45-day sampling season, with one data logger for each sub-site. Minimum, maximum, mean and standard deviations were computed. Microtopography of bogs is a known proxy of soil hygrometry (Rydin et al., 2013) and was measured through drone photography (model: ©FC6310S 8.8 mm; flight altitude 55 m; Resolution of 1.4 cm/px and altitude precision to the level of 1 cm). A five meter buffer around

each sampling point was assessed and variations in the microtopography were calculated along with the rugosity index (based on the ruggedness index of topographic heterogeneity by Riley et al., 1999 with GIS QGIS.org, 2022). Mean, standard deviation, delta between minimum and maximum height of topography as well as mean and standard deviation of the rugosity index were also calculated.

Landscape variables were assessed through GIS after mapping the different habitats in a 500 m radius around the sampling points (mapped based on 2012 aerial images at 1 m resolution from BD ORTHO®). Minimal distance between habitats common to all sites (*Abies balsamea* dominated forests, ponds and pools) as well as the surfaced covered by every present habitat (m<sup>2</sup>) in each trap's 500 m buffer was assessed.

### 2.5. Functional traits

Two criteria were set to select the traits: (1) they must be reported as drivers of species assemblages and (2) they must be available in published literature. The functional trait definition provided by Violle et al. (2007) and followed by Wong et al. (2019) was used, with the exclusion of environmental preferences as they are not, strictly speaking, a functional trait. Three traits were selected for spiders: dispersal abilities (ballooning), body size and trophic guild. For vascular plants, dispersal mode (by water, wind, zoochory and vegetative local dispersal), seed mass, plant height and SLA (specific leaf area) were chosen. These traits are known to be linked to environmental responses in both spiders (Schirmel et al., 2012) and in vegetation (Garnier and Navas, 2012; Laine et al., 2021). When these traits were not present in the literature, the value from the closest species within the genus was used.

2.6. Statistical analysis

Potential pattern in diversity metrics (TD & FD, alpha and beta) between sites were assessed with rarefaction curved from iNEXT.3D (Chao et al., 2021) and iNEXT.beta3D packages (Chao et al., 2023). This method was selected to account for the possible influences of sampling coverage and dominance patterns through the comparison of different diversity orders (Hills number of  $q = 0; 1; 2$ ). The tests were run with 40 knots and 200 bootstrap replications. Potential significant differences were assessed through the absence of overlapping confidence intervals on iNEXT.3D curves (Chao et al., 2014).

To assess trait association with a site's specificity, three matrices were analyzed simultaneously through an RLQ analysis containing the following information: L (species abundance across samples), R (environmental characteristics of samples) and Q (species traits), which crosses traits and environmental variables weighted by species abundances. For this, the RLQ function of ade4 package (Dray and Dufour, 2007) was used. In addition, following the method in Borcard et al. (2018), a Fourth corner analysis was done to assess the pairwise relationships between traits and environmental variables as a complementary method to the RLQ as proposed by Dray et al., (2012, 2014) as it

allows to link the traits and environment matrices that were both tied to the assemblage matrix within the RQL.

To assess the relative importance of local and landscape variables, alpha diversity, and multiple regressions were done with a stepwise model selection procedure by AIC (Akaike, 1974), implemented in the MASS R package (Venables and Ripley, 2002) on rarefied taxonomic and functional diversity based on Chaos estimator with the BAT package (Cardoso et al., 2015). Relative contributions of explicative variables to the model were estimated using the relaimpo package (Grömping, 2006) with the  $R^2$  contribution averaged over orderings among regressors (Lindeman et al., 1980; Chevan and Sutherland, 1991). To assess the relative importance of local and landscape impacts on spiders and vascular plants communities as well as on beta diversity (both taxonomic and functional) a variance partitioning was done following Borcard et al. (2018) and Lafage et al. (2015). Taxonomic beta diversity was based on Bray Curtis distance while functional distance matrices were based on kernel density n-dimensional hypervolume methods (Mammola and Cardoso, 2020) implanted in the BAT package (Cardoso et al., 2015). All data analyses were conducted using the free software R-3.6.2 (R Development Core Team, 2021).

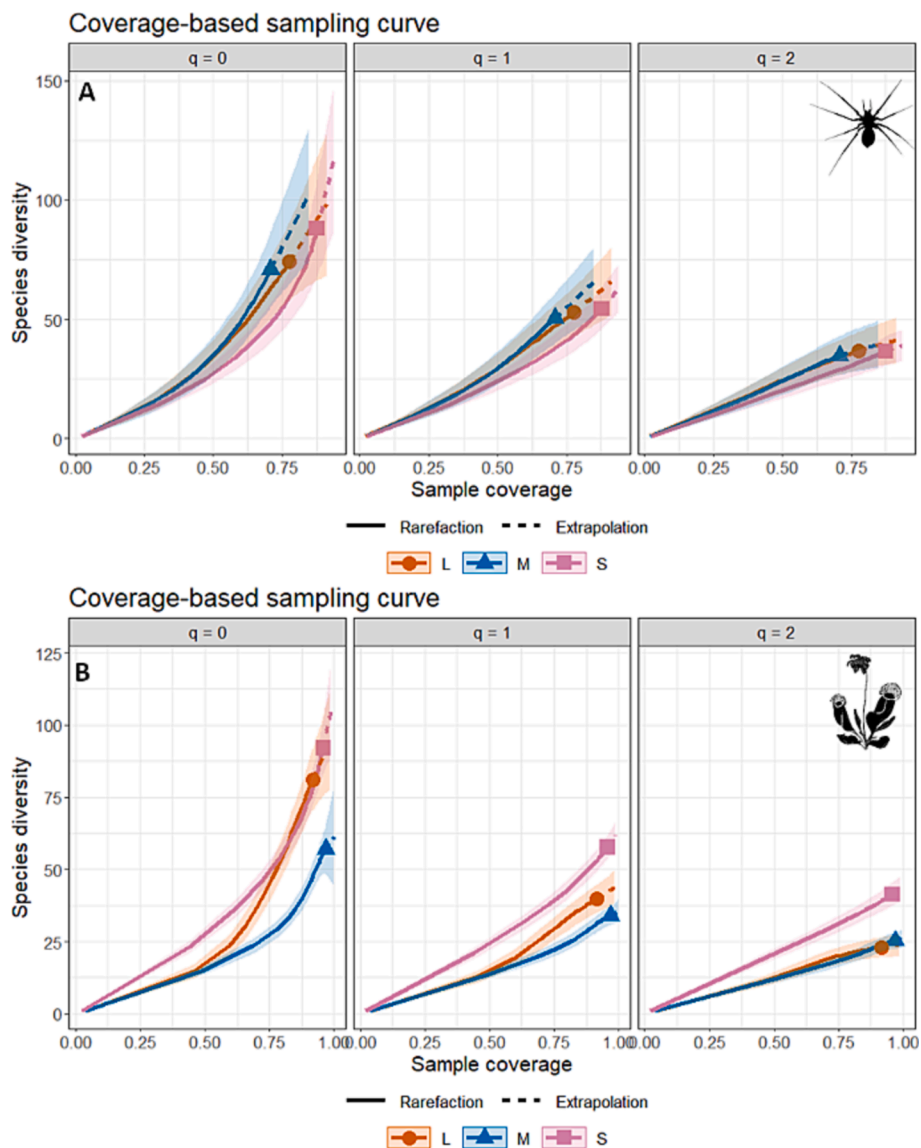


Fig. 2. Spider (A) and vegetation (B) alpha taxonomic diversity against sample coverage comparison between sites: S = St. Pierre; L = Langlade; M = Miquelon. The interval of confidences of each curve is based on a bootstrap following Chao et al. (2021).

### 3. Results

Taxonomic alpha diversity compared through rarefaction curves at different orders of diversity displayed contrasting results between spiders and vascular plants (Figs. 2 & 3; see Appendices A & B for the species lists and associated traits values per taxon for spiders and vascular plants respectively).

No significant differences were observed between sites in the spider assemblages regardless of the diversity order (Fig. 2). For vascular plants assemblages, a higher taxonomic diversity was observed in St. Pierre in the three orders, except for Langlade’s assemblages with  $q = 0$  that appear to be rich (Fig. 2.B)St. This pattern highlights that the previous differences between St. Pierre and Miquelon were not due to rare species alone but dominant ones as well. Lastly, it can be observed for  $q = 2$  (Fig. 2.B) that the plant assemblages from Langlade and Miquelon are not significantly different. On the other hand, the St. Pierre assemblages of vascular plants are higher in diversity with a pattern of dominance shared between more species.

This pattern was also observed for functional alpha diversity with no differences between sites for spider assemblages, regardless of the diversities’ orders and the same relationship between sites for each order of diversity of vascular plant assemblages (Fig. 3 A & B) with the exception of Langlade and Miquelon which are not being different for  $q = 1$  (Fig. 3.B).

Taxonomic beta diversity compared through rarefaction curves at different order of diversity displayed close patterns between spiders and vascular plants (Fig. 4, A&B). No significant differences were observed for  $q = 0$  and  $q = 1$  for both spider and vascular plants assemblages. For  $q = 2$ , spider assemblages were less divergent between Langlade and

Miquelon than between St. Pierre and Miquelon and St. Pierre and Langlade. No differences were observed for vascular plants at order  $q = 2$ .

Functional beta diversity compared through rarefaction curves at different orders of diversity also displayed close pattern between spiders and vascular plants (Fig. 4, C & D). No significant differences were observed for  $q = 0$ , while  $q = 1$  and 2 displayed patterns of differences with various degrees of strength. Spider beta diversity for both  $q = 1$  and  $q = 2$  displayed an intermediate pattern with St. Pierre and Miquelon differences being significantly higher than those of Miquelon and Langlade. The differences between St. Pierre and Langlade can be considered intermediate with no observable differences from the two other pairings. Vascular plants beta diversity for  $q = 1$  displayed a significantly lower divergence between Miquelon and Langlade than for the other two pairings of sites while  $q = 2$  displayed no differences.

#### 3.1. RLQ

Both spider and vascular plant assemblages displayed separated groupings with a specificity of the sub-site ZS1 being isolated from the rest of the St. Pierre assemblages and other sites (Figs. 5 & 7). One difference between the spiders and vascular plants was that the plant assemblages of Langlade and Miquelon were close together (Fig. 7).

For spiders, the first axis (81.54 % of projected inertia) separated the sub-site characterized by anthropogenic feature (ZS1 in St. Pierre) and the complex mosaics of natural landscapes (ZS2 and ZS3) from the more natural and homogeneous sites of Langlade and Miquelon (Fig. 5). The projected spider’s functional traits on this axis (Fig. 6.A) highlighted larger spiders - the sheet web weaver guild and ballooning spiders for the anthropogenic and complex landscapes, while natural sites were more linked to the guilds of specialist hunters, space web weavers and non-ballooning spiders. Along the same axis, the projected environmental variables (Fig. 6.C) were linked to cover of other habitats (forest, heath and coastal habitats) or anthropogenic ones such as roads and urban areas for the anthropogenic and complex landscapes while local topographic variable and humid habitat covers drive the right side, linked to the assemblages of natural habitats.

The second axis (12.31 % of projected inertia) separated the spider assemblages from Miquelon and Langlade. The projected traits associated to this separation linked Langlade’s spider assemblages to orb web weavers and ambush hunters while Miquelon’s assemblages were associated with space web weavers and specialists (Fig. 6.B). The projected environmental variables associated with Langlade’s spider assemblages (Fig. 6.D) were the cover of wet grassland and meteorological variables while those from Miquelon were tied to the distance of the nearest woodlands of both *Abies balsamea* and *Larix laricina* along with meteorological variables.

For the vascular plants, the first axis (71.13 % of projected inertia) also separated the natural sites (Langlade and Miquelon) from the anthropogenic and complex landscapes of St. Pierre (Fig. 7). The main functional trait of vascular plants projected along this axis was air dispersal, associated with St. Pierre’s vascular plant assemblages. The environmental variables projected on the first axis (Fig. 8.A) were linked to hydrology: microtopographic measures (maximum, median, minimum) and cover of wet habitats (ponds and bogs), all associated with natural sites, while the other sites were associated with the cover of different habitats (heathland, *Abies balsamea* forest, road, coastal vegetation and urbanized areas) and heterogeneity of microtopography (SD, mean, median and maximum rugosity) (Fig. 8.C).

The second axis (20.28 % of projected inertia), which distinguishes the vascular plant assemblages from sites close to urban areas, was associated with traits of light seeds, zoochory and close vegetative dispersal (Fig. 8.B). Likewise, the environmental factor associated with this segregation was the cover of an invasive plant, *Reynoutria japonica*, a species associated with disturbed areas and dense human occupation (Fig. 8.D; see Appendix C for numerical details of each RQL’s projected

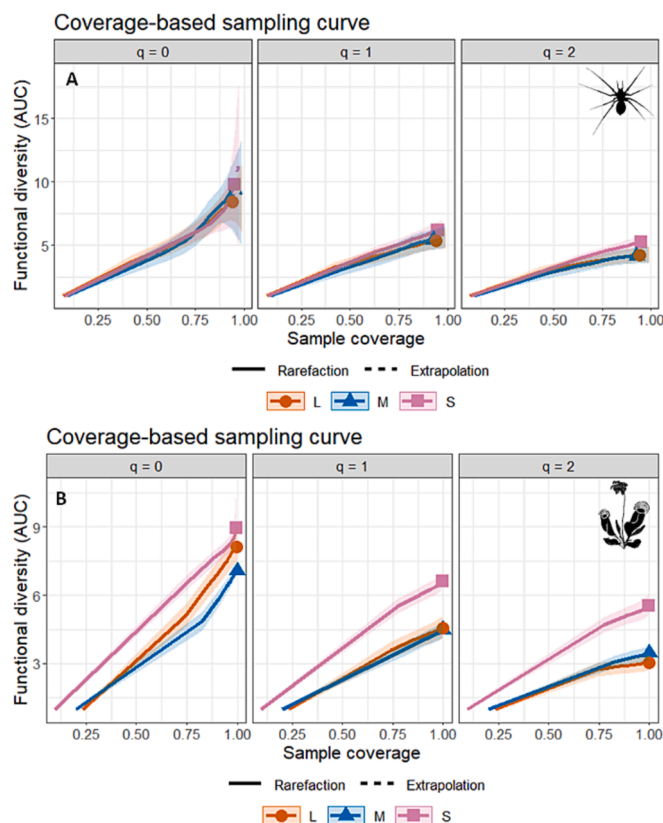
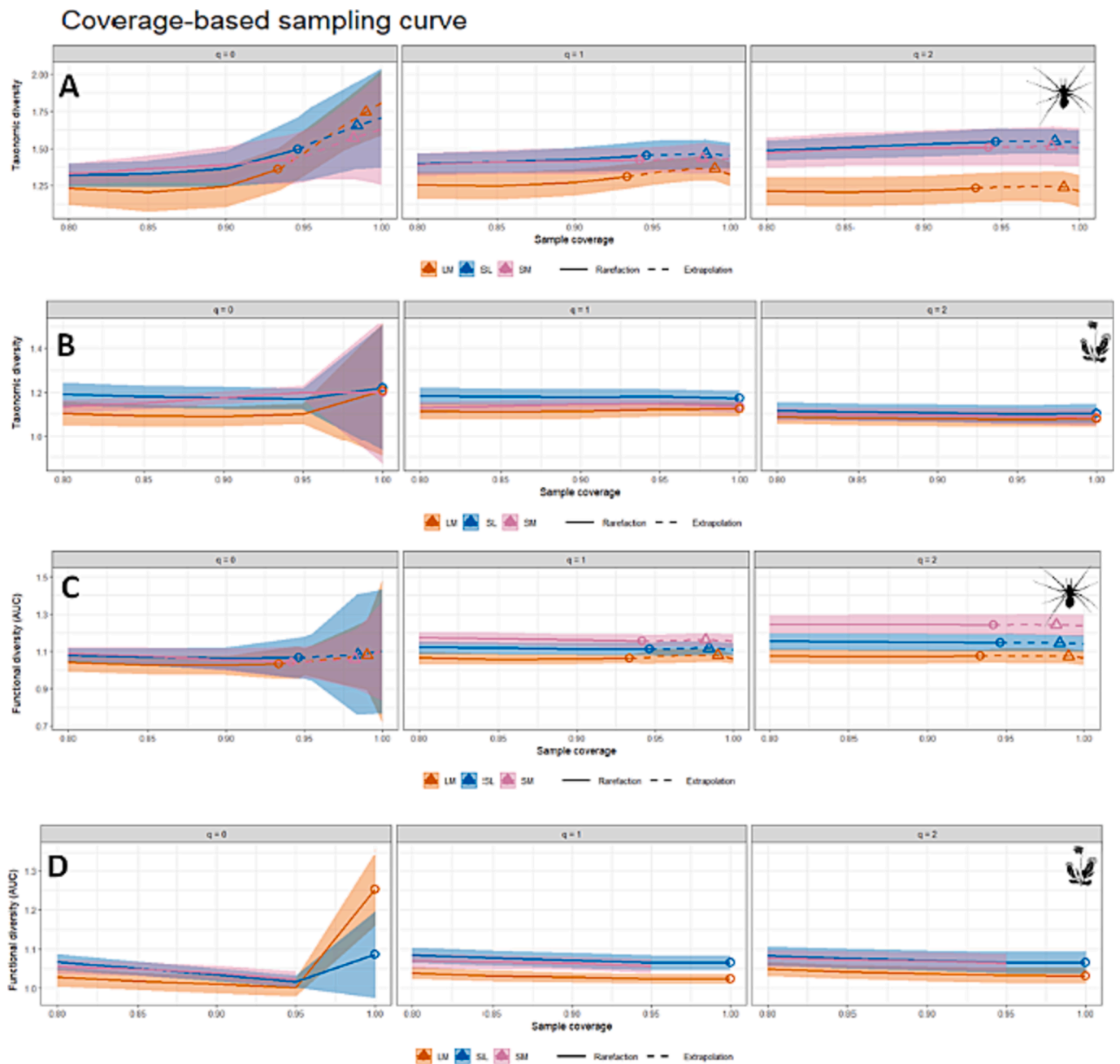


Fig. 3. Spider (A) and vegetation (B) functional diversity against sample coverage comparison between sites: S = St.Pierre; L = Langlade; M = Miquelon. Functional diversity AUC corresponding to the area under the curve for the functional distinctiveness profile based on functional diversity calculation from Chao et al. (2021). The interval of confidences of each curve is based on a bootstrap following Chao et al. (2021).



**Fig. 4.** Spider (A & C) and vegetation (B & D) beta taxonomic (A & B) and functional (C & D) diversity against sample coverage comparison between sites: S = St. Pierre; L = Langlede; M = Miquelon. Functional diversity AUC corresponding to the area under the curve for the functional distinctiveness profile based on functional diversity calculation from [Chao et al. \(2021\)](#). Confidence interval of each curve is based on a bootstrap following [Chao et al. \(2021\)](#).

weight values).

### 3.2. Fourth-Corner analysis

The fourth-corner analysis did not highlight any pairwise relationships between spider traits and other variables. For vascular plant assemblages, the mode of dispersal by wind was significantly and positively affected by SD and delta of topography, the mean, median, SD and maximum of rugosity and habitat cover of mild urbanization and halophyte vegetation.

### 3.3. Variance partitioning

The models largely explained spiders' taxonomic ( $R = 0.96$ ;  $p <$

$0.001$ ) and functional ( $R = 0.84$ ;  $p < 0.001$ ) diversities as well as and vascular plant alpha taxonomic ( $R = 0.36$ ;  $p < 0.001$ ) and functional ( $R = 0.65$ ;  $p < 0.001$ ) diversities. The local and landscape variable impacts of alpha diversity displayed contrasting responses between spiders and vascular plants ([Fig. 9](#)). While spiders responded to several variables for both taxonomic and functional diversities ([Fig. 9.A & B](#)), whereas vascular plants only responded to landscape variables ([Fig. 9.C & D](#)). Spider alpha diversity varied between taxonomic and functional with a slightly higher percentage attributed to landscape variables rather than local ones (53 % vs. 47 %) and a strongly higher percentage for landscape variables with functional diversity (74 % vs. 16 %). Spider alpha diversity was rather evenly distributed amongst landscape variables for both taxonomic and functional diversities while a striking 45 % of variance was attributed to the local variable “mean topography” in

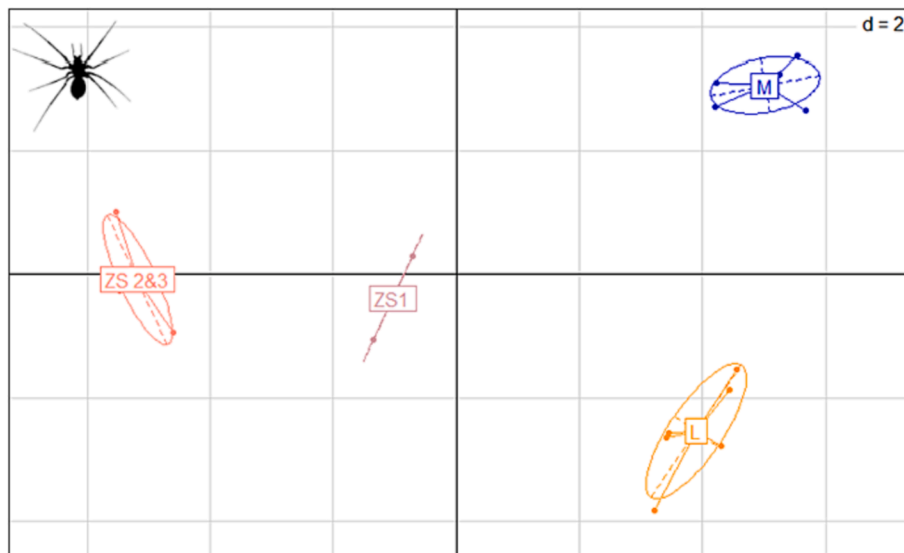


Fig. 5. 4 RLQ projection of spider assemblages. Sites L = Langlade; M = Miquelon; ZS1, ZS2 & ZS3 = the three sub sites of St. Pierre.

taxonomic diversity against a 16 % for functional diversity. Vascular plants' alpha diversities, both taxonomic and functional, responded to four landscapes variables. Taxonomic and functional diversities shared three variables: cover of urbanized habitat, of highly urbanized habitats and of bogs. Distance to wood was associated with taxonomic diversity and distance to ponds to functional diversity alone. It can be observed that between taxonomic and functional alpha diversity of vascular plants, there was a shift in the relative variance explained by the categories. Only 52 % of the variance was explained in the taxonomic diversity model and half of it was due to the distance to the nearest *Abies balsamea* forest while for functional diversity model, 78 % of the variance was explained and 42 % of it came from the combined cover of urbanized and strongly urbanized areas.

Regardless of the metrics, spider assemblages displayed higher variance explained overall than vascular plants (taxonomic: 99 % vs. 51 %; functional: 90 % vs. 78 %, spiders vs. plants respectively). The variance partitioning between local and landscape environmental variables both for spider and vascular plant assemblages' composition displayed a high interaction (Table 1) and indicated the stronger importance of landscape rather than local variables with various degrees of strength. Spider assemblages had a sevenfold higher influence from landscape versus local variables where it was only slightly higher for vascular plant assemblages. In the model selection, the spider assemblages displayed a sensitivity for the cover of humid grasslands and roads at the landscape scale, to the minimal rugosity of topography, and the mean and maximum temperature at the local scale. The vascular plant assemblage's model selected for the covers of ponds, humid grasslands and moderately urbanized areas at the landscape scale and minimal and standard deviation of rugosity as well as mean temperature at the local scale.

The variance partitioning between local and landscape environmental variables both for spiders and vascular plant beta diversity displayed higher variance proportions explained by landscape variables, with the exception of spider functional beta diversity for which no partition of variation was significant. Similarly, spider taxonomic beta diversity displayed higher differences between landscape and local proportions of variations explained, while a high proportion of the overall explained variation was linked to correlation between variables. In the model selection, the spider beta taxonomic diversity displayed a sensitivity for mean and standard deviation of height of microtopography, maximum temperature and mean and standard deviation of air humidity for local variables. Landscape variables for spider beta taxonomic diversity included cover of natural habitats (*Abies balsamea*

forests, heathlands, peat bogs, ponds, sea and *Larix laricina* forests) and urbanized habitats (highly urbanized area and ruderal vegetation) as well as distance from natural habitats (*Abies balsamea* forest, ponds and pools).

The vascular plants' beta taxonomic diversity displayed a sensitivity for mean, median and delta of height of microtopography, standard deviation of rugosity as well as mean and standard deviation of air humidity for local variables. Landscape variables for the vascular plants beta alpha diversity included cover of natural habitats (*Abies balsamea* forests, wet grasslands, peat bog, ponds and sea) and urbanized habitats (urbanized areas, roads, ruderal vegetation).

While it was not possible to make comparisons between spiders and vascular plant's functional beta diversity, a pattern was observable for vascular plant taxonomic and functional beta diversity. These were characterized by a higher proportion of variance explained by landscape variables. The beta functional diversity of vascular plants displayed a sensitivity for minimal, mean and standard deviation of temperature for local variable as well as distance to natural habitats (*Abies balsamea* forest, ponds and pools), cover of natural habitats (heathland, wet grasslands, peat bogs, ponds and streams) and cover of urbanized habitats (both ruderal vegetation and highly urbanized areas).

## 4. Discussion

### 4.1. Pattern of diversities

Spiders and vascular plants displayed similar responses for a given metric, but for a given taxon, metrics revealed different responses to changes in environmental conditions. The joint numerical response between taxonomic and functional diversity is not surprising considering their intrinsic mathematical relationship (Pavoine et al., 2013), but even though close to each other, taxonomic and functional diversity displayed varying patterns that may have ecological significance. Lack of differences between facets of spider alpha diversity was also reported in other ecological studies where spider assemblage's differences resided in turnover patterns without notable alpha diversity differences (Bell et al., 1998; Coccia and Fariña, 2019; Hacala et al., 2020). The pattern observed here is very likely to match previous results considering the marked dissociation of the communities in the RLQ community analysis. This first variation of responses between metrics highlights the complementarity of alpha and beta diversities in the context of our bogs, validating our hypothesis. The vascular plants assemblages, regardless of the metric used, had higher diversities within St. Pierre, only matched



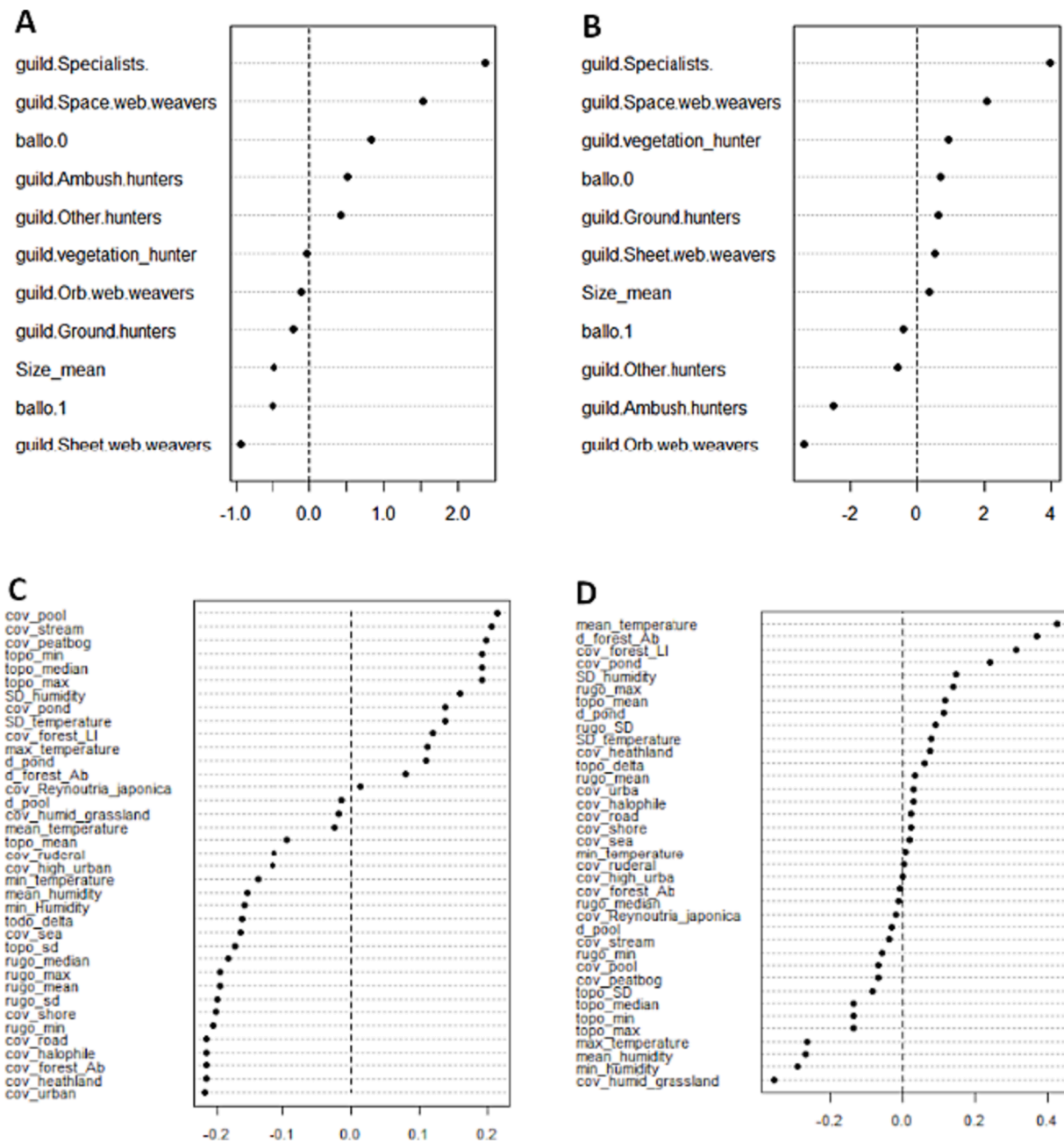


Fig. 6. The projected weight of each traits of spider’s assemblages link to the first (A) and second (B) axis and the projected weight of each environmental variable link to spider’s assemblages on the first (C) and second (D) axis. The dashed line was added to help visualize the 0.

by the assemblages from Langlade when considering richness, and highlighting the importance of rare vascular plant species in Langlade. It is known that ombrotrophic peat bogs close to the sea on the Atlantic Canadian Coast are more diverse due to the presences of species usually associated with poor minerotrophic peat bogs (Damman & Dowhan, 1981; Glaser, 1992). Additionally, the richer the peat bog, the more it is known to have its richness impacted by landscape heterogeneity (Vitt et al., 1995). One explanation of the higher vascular plant richness of St. Pierre sites could come from their greater proximity to the coast, enriching the bog. Likewise, the specific habitat mosaic around the St. Pierre sites is associated with higher topography which may also lead to bog enrichment through runoff after rains. One or both of those explanations could lead to an increased permeability in colonization from neighboring vascular plant habitats. Indeed, ZS2 and ZS3 higher diversities are linked to species often associated with other habitats (e.g.

*Dantonía spicata*, *Sanguisorba canadensis* and *Abies balsamea*). The lower richness of ZS1 could be linked to the influence of adjacent urban areas as expected at this spatial scale (Bonn et al., 2016) yet further measurement to assess such impacts might be required to demonstrate more conclusive results.

The relationship between the diversities of vascular plant assemblages of the more natural habitats of Langlade and Miquelon revealed the patterns of sites specificities. The higher taxonomic Shannon diversity of Langlade vascular plant assemblage over that of Miquelon is observed as well with taxonomic richness but not with Simpson taxonomic diversity. These results highlight the importance of rare species within Langlade assemblages while Miquelon ones have no species that are not present at least in one of the other two sites. Those rare species unique to Langlade have high degrees of specialization (Payette and Rochefort, 2001) and this would appear to indicate local factors rather

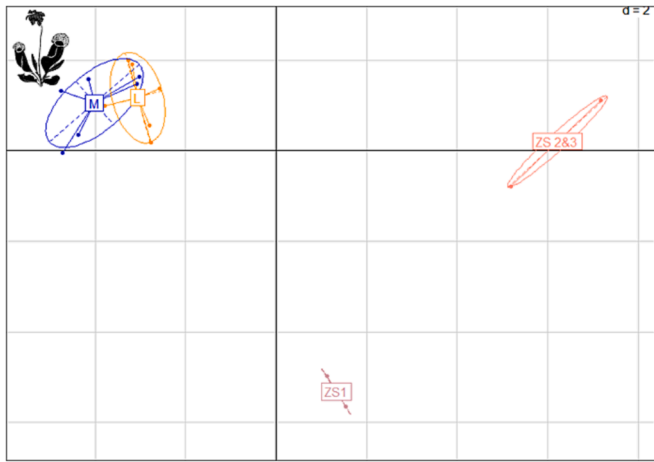


Fig. 7. RLQ projection of vascular plant assemblages. Sites L = Langlade; M = Miquelon; ZS1, ZS2 & ZS3 = the three sub sites of St. Pierre.

than colonization by surrounding habitats species. In addition, when dominant species are given more weight through Simpson diversity, Langlade and Miquelon’s assemblages display no differences in

taxonomic diversity. This pattern was expected as dominant bog specialist sedges like *Trichophorum cespitosum* (Payette and Rochefort, 2001) lower the evenness. When considering functional diversities, the Shannon diversity patterns between Langlade and Miquelon resemble the Simpson one which indicates a global functional redundancy. This is to be expected in a habitat as harsh as a bog (Robroek et al., 2017).

The variation of sensitivity and therefore responses of our taxa and metrics here indicate how their potential as ecological indicators is displayed. The richness inclined response of vascular plants makes up for the low evenness and dominated assemblages in harsh habitats, like those found in bogs.

#### 4.2. The Composition, traits and environment

The RLQ analysis highlighted differences in assemblages between all sites for both taxa with the only exception of Langlade and Miquelon for which vascular plants assemblages were close together. This general pattern of differences indicates that even within a small archipelago, in closely comparable habitats with high environmental filters, there can be a high variation in composition. The closeness of Miquelon and Langlade here echoes the diversity pattern described earlier with the beta diversity curves and the shared dominant species. Another assemblage divergence observed is the separation of the ZS1 from the two other sub-sites of St. Pierre with both taxa. This pattern was discussed

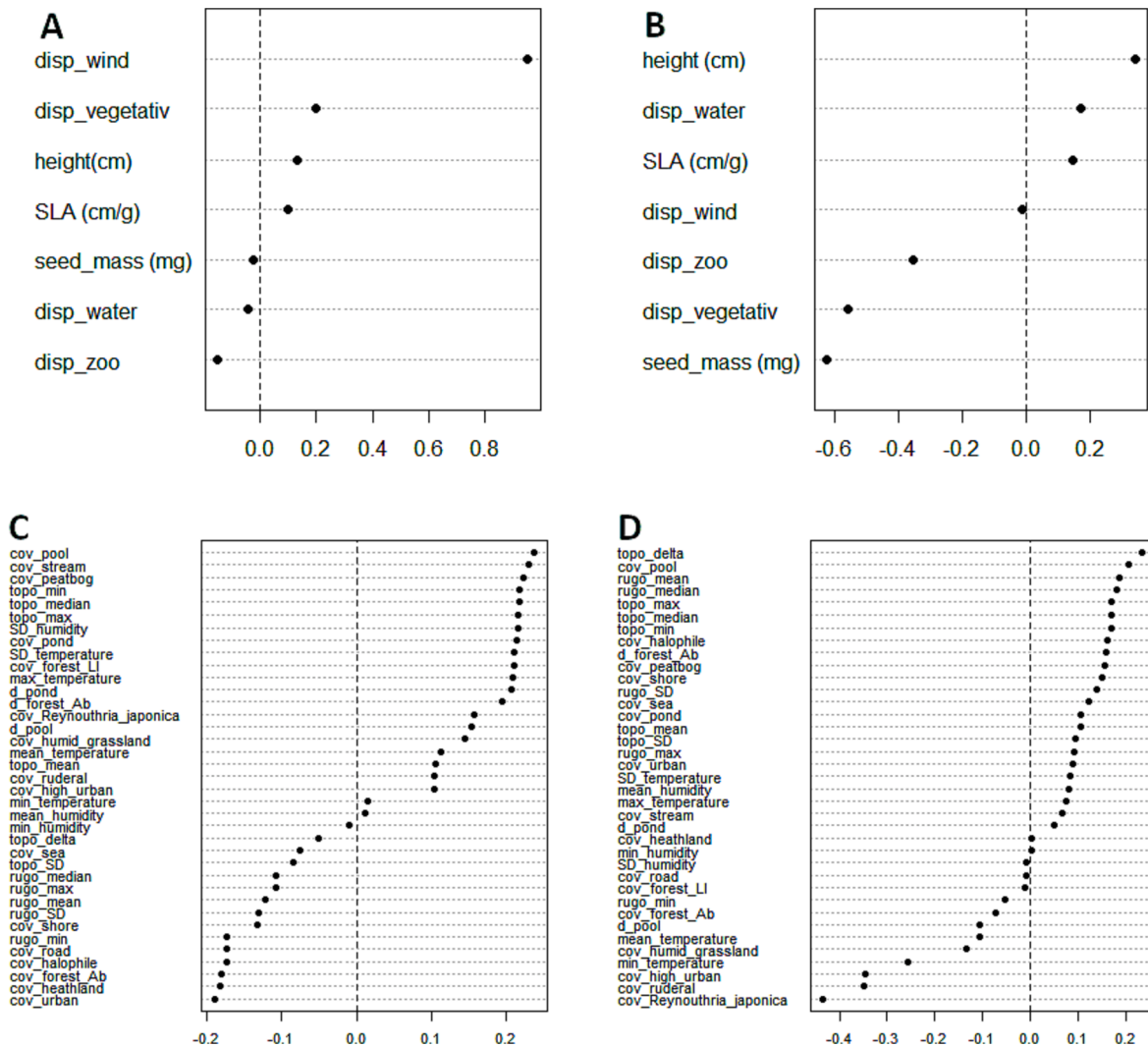


Fig. 8. The projected weight of each trait of vascular plants assemblages links to the first (A) and second (B) axis and the projected weight of each environmental variable links to vascular plants assemblages on the first (C) and second (D) axis. The dashed line was added to help visualizing the zero.

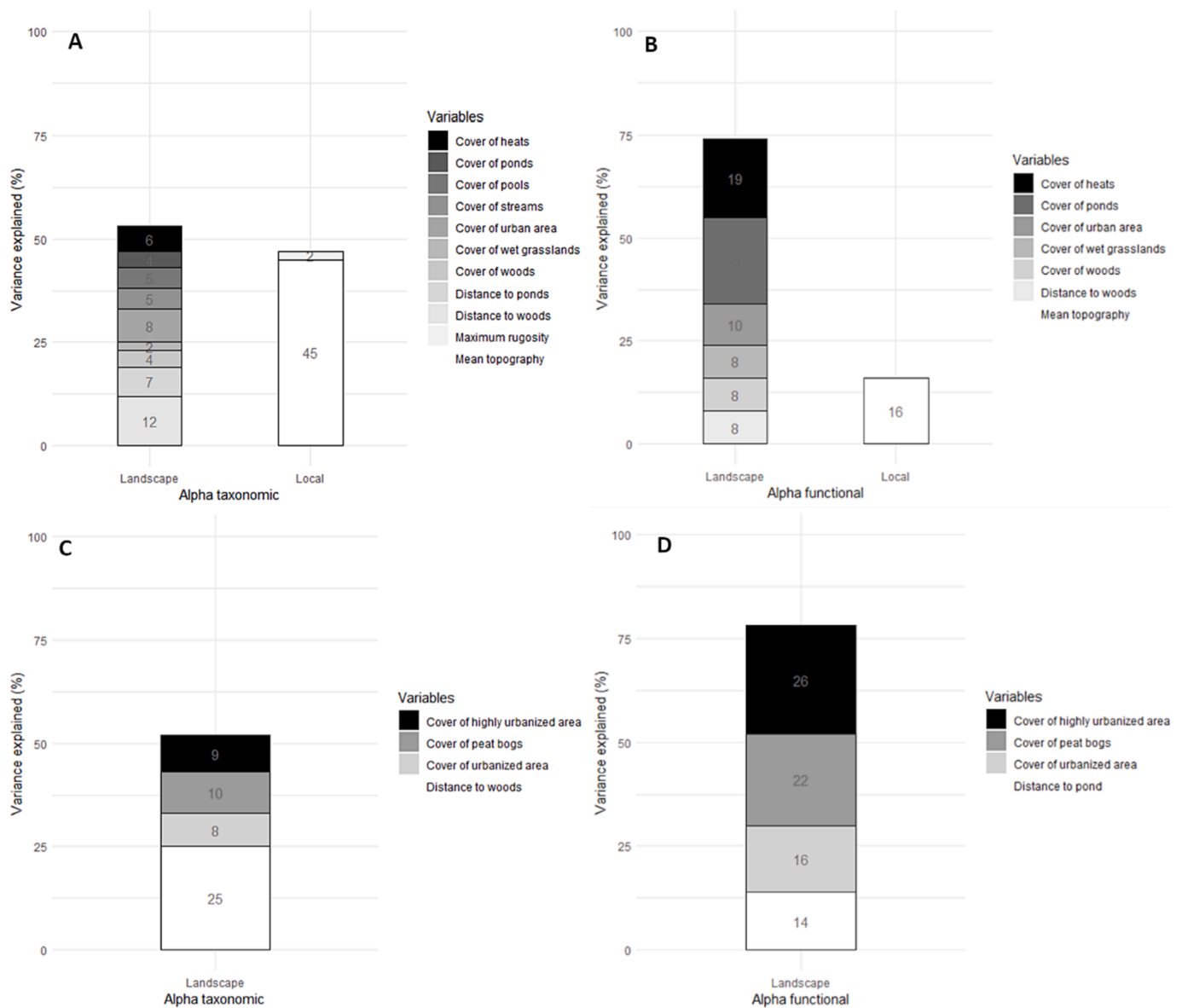


Fig. 9. The relative variance explained by environmental variables in alpha diversity models for: (A) Spider taxonomic diversity; (B) Spider functional diversity; (C) Vascular plant taxonomic diversity; (D) Vascular plant functional diversity.

Table 1

Variance partitions between landscape and local variables for community and beta diversity following Borcard et al. (2018). Statistical significance threshold of each partition was set for  $p < 0.05$  \*,  $0.01$  \*\*,  $0.001$  \*\*\*. NA value corresponds to models that failed to converge.

| Variance partitions          | Local |     | shared | landscape |     | unexplained |
|------------------------------|-------|-----|--------|-----------|-----|-------------|
| Composition                  |       |     |        |           |     |             |
| Spider                       | 1 %   | *** | 22 %   | 7 %       | *** | 70 %        |
| Vegetation                   | 5 %   | *** | 29 %   | 8 %       | *** | 58 %        |
| Taxonomic $\beta$ diversity  |       |     |        |           |     |             |
| Spider                       | 7 %   | *** | 32 %   | 29 %      | *** | 32 %        |
| Vegetation                   | 14 %  | *** | 45 %   | 20 %      | *** | 21 %        |
| Functional $\beta$ diversity |       |     |        |           |     |             |
| Spider                       | NA    |     | NA     | NA        |     | NA          |
| Vegetation                   | 8 %   | *** | 17 %   | 32 %      | *** | 43 %        |

through the lower richness of this sub-site in the vascular plants' assemblages, this is also seen with the spiders and the disturbances may be an explanation for this pattern as well (Pétillon and Garbutt, 2008). Indeed, the reduced richness of arthropod assemblages in disturbed

settings is an inconsistent response discussed in the literature (lower in Pétillon and Garbutt, 2008 and unchanged in Hacala et al., 2020). However, a highly stressful environment found in many bogs may filter out generalist species that compensate species loss in other perturbed environments, leading to the assemblages of both taxa being potential indicators of disturbance with the bog.

The RLQ analysis highlighted links between this sub-site and both environmental variables and traits of the associated assemblages. For the spider assemblages, the link is unclear for the ZS1 sub-site as it is in an alignment with the rest of St. Pierre sub-sites in the RLQ. As a whole, they are associated with sheet web weavers, ballooning spiders and bigger spiders. The sheet web weavers from St. Pierre assemblages are known to inhabit woodlands and open habitats (e.g. *Agelenopsis utahana*: Paison, 1997, and several Linyphiidae species like *Bathyphantes pallidus*: Buddle, 2001). The environmental variables associated with those assemblages are the cover of surrounding habitats including the *Abies balsamea* forest, subarctic heathland, and the coastal and urban areas. These results highlight the effects of the surrounding habitats that allow for spider colonization in an undisturbed bog, as they can manage the bog conditions without being specialists. Another explanation may be

derived from the interaction of an edge effect in a smaller bog in a complex landscape since edges of bogs are known to have reduced environmental filters (Payette and Rochefort, 2001) facilitating colonization by surrounding spiders. Thus, the variations within the spider compositions appears to be an indicator of the influence of the landscape matrix settings on the bogs.

The vascular plant assemblages associated traits and environmental variables for St. Pierre sites, contrary to spiders, are different between the ZS1 sub-site from that of ZS2 and ZS3. The variable that drove ZS2 and ZS3 vascular plant assemblages are rugosity measures of microtopography and cover of the different neighboring habitats. The local heterogeneity together with the impacts of both forest, heath and sea in the landscape concur with our previous hypothesis. Thus they may be enriched due to the closeness of the sea (Damman and Dowhan, 1981), which may reduce the filters which ease the colonization from pools of species in adjacent habitats. The sensitivity of vascular plant assemblages to local parameters of heterogeneity could be linked to edges effects and enhanced diversities by increasing the number of ecological niches within the bog, thereby affecting the composition of the assemblages (Thuiller et al., 2006). The one trait associated with those sub-sites is dispersal by wind. As noted in the literature, shrubs and tree species are among the most likely species to disperse from wind and from surrounding habitats into a peat bog (Campbell et al., 2003). Likewise, St. Pierre sites are characterized by the higher abundance of species tolerant to bogs but thriving in other habitats like *Abies balsamea* and Ericaceae shrubs like *Rhododendron groenlandicum*. Only the results from the Fourth corner analysis linking wind dispersal to environmental variables might not be due to direct impacts from the environment or adaptation but rather a correlation to St. Pierre sites as the environmental variables are all higher for these sites and the wind dispersal trait is the one associated to its assemblage. For the ZS1 assemblages, the main traits are small seed mass and vegetative dispersion. For the vascular plants, this sub-site is distinct from the others due to the absence of species rather than their presence, it is thus futile to draw any conclusions about these traits.

The two most natural sites are set apart from St. Pierre in the RLQ through a pattern linked to guild traits (specialist and space web weaver) and non-ballooning species. The guild traits associated with both sites were likely statistical artefacts as they were only represented by few individuals. Indeed, it is known that multivariate analysis such as that of the RLQ are sensitive to rare occurrences (Cao et al., 2001). However, the non-ballooning trait may be explained by specialist bog species that would not be prone to passive long-distance dispersal which would allow them to stray, as observed with spiders in other constraining habitats (Bonte et al., 2003). All environmental variables globally associated with the sites on Langlade and Miquelon were linked to hydrology, whether it was local with microtopography (Payette and Rochefort, 2001) or at the landscape scale and including ponds, streams and the bogs themselves. Such a sensitivity echoes commensurate findings within similar geographical and environmental contexts (Pelletier et al., 2009). This pattern highlights how spider assemblages are good indicators within natural bogs for they are less impacted by other habitats and are linked to the prevalence of water within ecosystems.

When considering vascular plants, the sites of Langlade and Miquelon were not separated by any specific traits but the same environment variables of the spiders, the hydrological variables. This concurs with bogs being rather homogeneous in their traits along geographical gradients (Robroek et al., 2017) while composition can vary, seen here through the variability of hydrology between landscapes which is a known key driver within peat bogs (Rydin and Juglum, 2013).

The assemblages of Langlade and Miquelon displayed differences on the RLQ for spiders only and were overlapping for vascular plants. The differences between Langlade and Miquelon for spider assemblages were linked to both traits and their environments but the traits were the same guild represented by too few individuals to be considered a robust pattern. The environment variables driving the differences between the

spider assemblages of the two sites are linked to landscape composition. Spiders from Miquelon appear sensitive to the distance to the nearest forest of *Abies balsamea* and the cover of *Larix laricina* while those of Langlade are linked to wet grasslands cover. Amongst the species only present in Miquelon, one of the more abundant was *Neoantistea agilis*, a species associated with forests near open water (Draney, 1997). Likewise, amongst the species only found in Langlade, there are species associated not only with bogs but open wet habitats like *Arctosa raptor* (Koponen, 1994).

Confirming our previous results, the variance partitioning displayed an important part of the variances explained by the landscape variables. The spider's assemblages and beta diversity's higher ratio (one to seven for the community and four to one point five for beta taxonomic diversity) highlight their higher sensitivity to landscape contexts rather than to vegetation (Lafage et al., 2015). This could be linked to the fundamental differences between spiders and plants, as spiders are mobile (Gerlach et al., 2013) and less dependent on water chemistry (Bonn et al., 2016), they are potentially less impacted by local environmental filters than plants are. On the other hand, the alpha diversity of vascular plants was only associated with landscape variables, whereas spiders responded to both local and landscape factors. This result resonates with the higher alpha richness pattern observed for St. Pierre's site. It could be linked to the landscapes that enriched the bog and added fen-related species, as the variables selected by the models are those associated with St. Pierre sites. It should also be noted that the greatest part of the explained variance is associated with the interaction of the landscape and local variables, highlighting the interwoven nature of these scales within peat bogs. This interconnectedness might be the source of the low and absent responses of the Fourth corner analysis as it tests for pairwise responses between traits and environmental variables and cannot assess their joint effects.

#### 4.3. Conclusion

This paper explored the use of multi-metrics and multiple taxa ecological indicators as they represent the complexity of natural environments. Concurring with our first hypothesis, vascular plant and spider assemblages displayed different responses which explain several aspects of the environmental settings examined here. This complementarity of indicators expresses itself through the respective sensitivity of the metrics used as they capture different angles of the studied system's ecology. The complementarities expected in hypotheses 1, 3 and 4 interact collectively. The redundancy of hypothesis 2 linked to the harsh nature of bogs was also observed, yet within the redundancy, the trait approaches within beta diversity consolidated our understanding of beta diversity pattern. This multi-taxon and multi-metric approach highlights the complementarity of different indicators and their respective sensitivities, providing insight on their potential future application and use in bog conservation and restoration status studies or the assessment of environmental disturbances. Indeed, this study highlights peat bogs' sensitivity to many intertwined environmental cues and suggests methods to untangle them. Faced with the urgency of peat bog conservation and restoration that requires an ability to assess habitat dynamics, such methods are paramount (Bonn et al., 2016). Likewise, a better understanding of bogs within their landscapes could help for conservation prioritization as the landscape context is known to be impactful (Payette and Rochefort, 2001). A potential next step toward further improvements in related studies should employ multiply joint indicators. A known complementarity within measures of diversity could be the addition of phylogenetic diversity (Cadotte et al., 2013; Hacala et al., 2021; Ridel et al., 2021), as diversity metrics has proven to be an important tool of biodiversity conservation (Faith, 1992; Rodrigues et al., 2005). Another improvement could come from adding taxa associated with different scales and environmental processes and with a different trophic regime which could lead to a better understanding through complementarity. Oribatid mites are recognized as indicator

taxa in peat bogs (Lehmitz et al., 2020; Behan-Pelletier & Lindo, 2023). Yet they are a relatively poorly known taxa (Behan-Pelletier & Lindo, 2019) and should be tested in future similar studies. Their use could make an important addition to the models used here to improve both our knowledge of bog biodiversity as well as the multitaxa indicator as a tools.

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## CRedit authorship contribution statement

**Axel Hacala:** Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Writing – original draft, Writing – review & editing. **Manuel Salgueiro-Simon:** Formal analysis. **Allison Bain:** Conceptualization, Funding acquisition, Project administration, Supervision, Writing – review & editing. **Dominique Marguerie:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – review & editing. **Julien Pétilion:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – review & editing.

## 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.

## Data availability

Data will be made available on request.

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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.2023.111389>.

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