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Research Article

Keywords: Alkaline fens, Cladium mariscus, Phenotypic plasticity, Vegetation dynamics, Adaptive management

Posted Date: January 23rd, 2026

DOI: https://doi.org/10.21203/rs.3.rs-8646833/v1

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Title

***Cladium mariscus* Phenotypes are driven by Management but Influence Vegetation Dynamics in Northern France Alkaline Fens**

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Acknowledgements

The authors thank the teams that participated to field work and site monitoring, including A. Gazaix, A. Janczak, M. Castelli, G. Jacek, N. Caron, W. Cheyrezy, A. Pencoat-Jones, V. Lecocq, G. Gaudin, Q. Rousseau and Q. Marescaux ; the Conservatoire d'espaces naturels des Hauts-de-France for site management and the project coordination, the Conservatoire Botanique National de Bailleul for the expertise on vegetation, the Parc Naturel Régional Scarpe-Escaut for assisting the field work in Marchiennes, and the Conseil départemental de l'Oise as landowner of Sacy peatland. The authors particularly thank Mikk Espenberg for the invitation to submit this research.

Abstract

Large peatland areas throughout the world have been degraded, contributed to climate change, biodiversity crisis and ecosystem services no longer provided. Their restoration and long-term conservation remain challenging due to anthropogenic pressures and environmental variability. This study investigates the phenotypic plasticity and vegetation dynamics of *C. mariscus* populations across four restored alkaline fens in Northern France. Field surveys conducted in 2021 and 2024 assessed morphological traits, species composition, and environmental variables such as moisture and trophic conditions. The results reveal two distinct phenotypic strategies: a competitive strategy characterized by dense vegetation, thick litter layers, and low flowering rates in mature stands, and a colonizer strategy marked by higher flowering rates and lower density in

disturbed or younger sites. Vegetation surveys further highlight how water level fluctuations, nutrient availability, and management practices influence community composition and habitat conservation status. These findings underscore the importance of adaptive management strategies that balance biodiversity conservation with the ecological requirements of *C. mariscus* populations. The study contributes to a broader understanding of phenotypic plasticity in a dominant wetland species and provides actionable insights for the restoration and management of alkaline fens in the context of climate change and eutrophication.

Keywords: Alkaline fens, *Cladium mariscus*, Phenotypic plasticity, Vegetation dynamics, Adaptive management

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1. Introduction

Peatlands cover 3% of the Earth's surface but store about one third of soil carbon (Joosten et al. 2012). Hosting a threatened biodiversity and providing habitats for endangered species, their structural and functional integrity is critical for maintaining biodiversity (Minayeva et al. 2017). In the most urbanized parts of the world, large areas of peatlands have been drained, extracted, converted to crop land and pastures (Joosten et al. 2012). Large amounts of peat have already been mineralized, contributing to a long-term release of greenhouse gas, the decline of the peatland biodiversity, and a decrease of ecosystem services (e.g. water, nutrient, solid fluxes regulation; Leifeld & Menichetti 2018). On the other hand, most peatland in less populated areas are still undamaged, although they can undergo global processes like global warning or eutrophication (Gallego-Sala et al. 2018; Limpens et al. 2008). Alkaline fens are among the most threatened wetland ecosystems in Europe, recognized for their ecological value (Nilsson, 2016; Seer & Schrautzer 2014). These ecosystems are characterized by calcium-rich soils, unique hydrological regimes, and specialized flora, including *Cladium mariscus* (Great fen-sedge), a species that plays a pivotal role in peat formation and carbon sequestration (Bensettiti et al. 2002). Despite their ecological importance, alkaline fens have undergone significant degradation over the past century due to drainage, agricultural intensification, and eutrophication (Tanneberger et al. 2017), since they are located near coasts or large and densely populated valleys. During the last decades (Apori et al. 2022), restoration projects have been implemented to reverse this decline by re-establishing hydrological regimes and reducing nutrient inputs (Zedler & Kercher 2005). One way of restoration consists of restoring a vegetation adapted to develop in harsh environments, where organic matter degradation cycles are interrupted by a constant moisture and a lack of nutrients, with adapted management (Martens et al. 2023). This vegetation is then capable to accumulate and produce the peat, contributing to carbon storage by ecosystems (Loisel et al. 2014). It is often characterized by plants sharing several traits adapted to this environment and modifying the ecological processes of the ecosystem, like competition with other species as a main driver (Hinzke et al. 2022).

Phenotypic plasticity—the capacity of a single genotype to express varying phenotypes in response to environmental conditions—is increasingly recognized as a key mechanism for the resilience of wetland species (Nicotra et al. 2010; Richards et al. 2006). For *C. mariscus*, phenotypic plasticity may enable populations to adapt to fluctuating water levels, nutrient

availability, and management practices, as shown for *Cladium mariscus* (Conway 1936; Namura-Ochalska 2005), *C. jamaicense* (Richards & Olivas 2020) or other dominant plant species (Hinzke et al. 2022). Plants can also develop a phenotypic plasticity, to face environmental conditions (Ghalambor et al. 2007; Nicotra et al. 2010; Valladares et al. 2007), but to also face interaction processes like intraspecific (Cahill et al. 2010; Schmitt et al. 1995; Weiner 2004) or interspecific (Agrawal 2007; Callaway et al. 2002; Pierik et al. 2013) competition. These mechanisms allow to a pool of plant species to assemble in a same location, determining an assemblage potentially sharing common functional traits (Diaz et al. 2016; Lavorel et al. 2007; Violle et al. 2007), traits that provide a capacity to survive undergoing the conditions (Laughlin et al. 2020; Sobral 2021). However, the interplay between phenotypic variability, vegetation dynamics, and conservation status in restored alkaline fens remains poorly understood (Lamers et al. 2015). As underlined by several studies (Bruelheide et al. 2018; Coulombel 2020), if the response of functional traits to environmental gradients is well studied although sometimes incomplete (Kraft et al. 2015) or the conservation status only described with disturbances and assemblages (Bensettiti et al. 2002), the link between a trait of an engineer species like *C. mariscus* and the vegetation or its conservation status is still poorly studied. This study seeks to address this knowledge gap by examining how *C. mariscus* populations respond to environmental gradients across four restored sites in Northern France.

The primary objectives of this study are to:

1. Assess phenotypic variability in *C. mariscus* populations across sites with differing environmental conditions and management histories.
2. Analyze vegetation dynamics and community composition in relation to environmental variables, namely moisture and eutrophication.
3. Discuss the implications of these findings for the adaptive management and long-term conservation of alkaline fens.

By integrating field surveys, morphological trait analyses, and environmental data, this study provides insights into the ecological strategies employed by *C. mariscus* and their relevance for wetland restoration and conservation.

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2. Materials and Methods

2.1 Study Sites

This study was conducted across four alkaline fen sites in Northern France (Figure 1A), all of which are part of a restoration project. The sites were selected to represent a gradient of environmental conditions and management practices. The Marais de Sacy and Marais Nivart (hereafter marais de la Souche) are characterized by dense *C. mariscus* stands and minimal disturbance, while the Marais de Villiers is subject to rotational mowing and Tourbière de Marchiennes has experienced historical agricultural influence. These sites provide an opportunity to examine how phenotypic plasticity and vegetation dynamics vary in response to differing

levels of disturbance and hydrological regimes. The sites are all supplied with alkaline groundwater (Caron et al. 2020; Decodts & Pencoat-Jones 2020; Fourmy et al. 2022; Lecocq et al. 2024).

2.2 Environmental variables

Water levels were measured in each site hourly with automated dataloggers between July 2022 and April 2023. This data was corrected for atmospheric pressure with automated barometers, allowing an approximate accuracy of 15 mm. Each of these piezometers was placed to measure the fluctuation of the alluvial aquifer, i.e. the aquifer that interact with the soil surface and the vegetation and placed at a maximal depth of one meter. Nitrate concentrations were measured on different piezometers located nearby the site and measuring the groundwater parameters of the aquifer supplying each site, and available in the public and open database ADES (Winckel et al. 2022). We selected a direct measure of the groundwater nitrate content, as it did not interfere with vegetation, contrary to surface water samplings. The list of the selected piezometers is provided in supplementary table 1.

2.3 Field Surveys

Field surveys were conducted during the last week of August in 2021 and 2024 to coincide with peak vegetation growth and flowering. At each study site, two transects were established, and three 4 m² (2 × 2 m) quadrats were systematically sampled along each transect. To sample the exact location between the two sessions, the beginning and the end of each transect were marked with a 2m high bamboo stick.

Within each quadrat, a comprehensive set of data was recorded to characterize vegetation structure, species composition, and environmental conditions. Vegetation composition was documented through a full floristic survey, with species cover estimated using the Braun-Blanquet scale. Morphological traits of *C. mariscus* were measured including the leaf length and the litter thickness (recorded 9 times per quadrat, at each corner, at the middle of edges and at the center of the quadrat) using a straight bamboo stick marked with centimeter units. Reproductive effort was quantified by counting the number of flowering stems, both for the current (green stems) and previous (dry stems) years, within each quadrat. To estimate population density, two 0.25 m² (0.5 × 0.5 m) sub-quadrats were sampled within each 4 m² quadrat, and the number of living *C. mariscus* stems was recorded (Figure 1B).

To capture a longer-term evolution of vegetations of each site, vegetation relevés of 25 m² (5 × 5 m) were performed around the transects but within the same vegetation facies from 2019 to 2025, with 7 relevés in Marchiennes, 20 in Sacy, 14 in Souche, and 18 in Villiers, totalizing 59 relevés.

2.4 Data Analysis

Site comparisons

We performed Kruskal-Wallis tests with a Bonferroni correction, and, while significant, a Dunn post-hoc test to test the differences of water levels of each site and the nutrient concentrations of the groundwater supplying the sites.

Phenotypic Variability

Morphological and reproductive traits (leaf length, litter thickness, density, number of flowering stems) were compared between sites and years using paired t-tests, the transects being placed at the exact same location.

Vegetation Dynamics and Community Composition

Community-weighted means (*CWMs*) for moisture (*CWM-H*) and trophic (*CWM-N*) functional traits of communities were calculated using the indicator values of Landolt (1977). These indices provide a quantitative measure of the environmental conditions experienced by the plant community (Mueller-Dombois & Ellenberg 1974), as designed by Kreyling et al. (2025). We performed a model selection based on AIC to detect among the value and the heterogeneity in each variable measured those that influence the most *CWM-H* and *CWM-N*. Species richness and conservation status were evaluated using the grid developed by Coulombel (2020), which assigns scores based on the presence of typical species, the cover of nitrophilous or invasive species, and signs of disturbance. We performed Wilcoxon rank tests to assess differences between sites and modelled the evolution of the vegetation traits using linear regressions.

Software

We used R software version 4.4.3 (R Core Team 2025) to perform all the analysis, the MuMIn package (Bartoń 2025) for model selection as well as the ggplot2 package (Wickham 2016) for data visualisation. Variables were scaled prior the model selection.

3. Results

3.1 Site variability

Sites have a significant variability in the water levels (Figure 2A) measured by piezometers relative to the soil surface as well as significant differences in nitrate concentrations (Figure 2B) received from groundwater supply, measured in piezometers nearby (Table 1). Marchiennes is the site with significant higher water levels and the most fluctuating but is supplied with low concentrated water in nitrates. Sacy and Souche are both fluctuating around the soil surface although Sacy has a mean water level aboveground while Souche has a mean water level belowground. These sites received intermediate to high (Grootjans et al. 2021; Kimberly et al 2013) but a similar nitrate concentrated groundwater. Villiers has a constant water level supply by a nitrate-enriched groundwater allowing a water level very close to the soil surface.

3.2 Phenotypic Variability in *Cladium mariscus*

The morphological traits of *C. mariscus* exhibited significant variability between sites and years, reflecting differing environmental conditions and management regimes (Figure 3). In dense, mature stands (Sacy and Souche), litter thickness showed a marked increase, from 35 ± 5 cm to 50 ± 4 cm (Figure 3A, $p < 0.001$), indicating ongoing litter accumulation in these undisturbed sites. Flowering stem density remained consistently low (Figure 3D), averaging 1–2 stems m^{-2}, suggesting a prioritization of vegetative growth over sexual reproduction. The density of *C. mariscus* (Figure 3C) and their leaf length (Figure 3B) did not significantly change between 2021 and 2024 for these sites.

In contrast, disturbed sites (Villiers and Marchiennes) exhibited thinner litter layers (25–30 cm), but increasing in Marchiennes ($p = 0.004$). However, these sites displayed higher flowering stem densities (5–20 stems m^{-2}, $p < 0.001$, Table 2), indicating sexual reproduction in response to disturbance. The differences in most phenotypic traits between dense and disturbed sites were statistically significant for several measured variables ($p < 0.05$), with Sacy and Souche or in a lesser extent, Villiers and Marchiennes, more similar (Table 2), highlighting *C. mariscus* growth strategies according to the site.

3.3 Vegetation Dynamics and Community Composition

Vegetation surveys revealed marked differences in species composition and community structure between sites. Species richness was significantly higher in disturbed sites (Villiers: $t = 5.16$, $p = 0.012$ and Marchiennes: $t = 6.70$, $p < 0.001$), where nitrophilous species such as *Mentha aquatica*, *Phragmites australis* or *Lythrum salicaria* were more prevalent. In contrast, dense *C. mariscus* stands exhibited lower species richness. Conservation status was positively correlated with litter thickness ($r = 0.54$, $p = 0.03$) and density ($r = 0.55$, $p = 0.03$), negatively correlated with flowering stem density ($r = -0.53$, $p = 0.03$) and uncorrelated with species richness ($r = 0.30$, $p = 0.25$). This suggests that dense, mature stands with thick litter layers are indicative of high conservation value, while disturbed sites with higher flowering rates status present a lower conservation value, with a potential change in species composition towards more nitrophilous species.

The model selection for the Community Weighted Means (*CWMs*) of moisture (*H*) and trophic (*N*) indices retains in each case the richness of the community into the most parsimonious model (Supplementary Table 2). Species richness correlated negatively with *CWM-H* (Figure 4A) but positively with *CWM-N* (Figure 4B), suggesting a deviation from a theoretical community composed by *C. mariscus* ($H = 5$, $N = 1$) as a unique species, and therefore probably involving a limitation in the use of these indices.

Villiers is a site significantly differing from the three other ones, both for moisture and trophic indices (Figure 5), while Marchiennes, Sacy and Souche show no significant differences, a higher *CWM-H*, reflecting a vegetation with an ecological optimum around 5.0, but a lesser *CWM-N*, reflecting a more oligotrophic vegetation. The higher *CWM-N* of Villiers can be explained by a higher nitrate content in the groundwater supplying the site (Figure 2B). However, since Villiers has more constant water levels, the *CWM-H* are unexpectedly low (Figure 2A). During the time span of the study, *CWMs* remained stable, with no significant increase or decrease, whatever the

site, suggesting either a too short time span to identify a significant change on vegetation, or unchanging trophic or moisture conditions.

4. Discussion

4.1 Phenotypic Strategies in *Cladium mariscus*

The results of this study reveal two distinct phenotypic strategies in *C. mariscus* populations, each associated with specific environmental conditions and management regimes. In dense, mature stands such as those observed in Sacy and Souche, *C. mariscus* exhibits traits consistent with a competitive strategy (Kunstler et al. 2016). These include dense vegetation, thick litter layers, and low flowering rates, all of which suggest an investment in survival and clonal reproduction. Such traits are characteristic of *K*-selected species, which thrive in stable environments with limited resources (MacArthur & Wilson 1967; Agrawal 2007). The thick litter layer in these sites likely suppresses competition from other species, thereby maintaining the dominance of *C. mariscus* and contributing to the high conservation status of the habitat (Gianoli & Palacio-López 2009).

In contrast, disturbed sites such as Villiers and Marchiennes exhibit traits associated with a colonizer strategy. Here, *C. mariscus* populations display higher flowering rates and lower density, indicative of an investment in sexual reproduction and dispersal (Zhang et al. 2023). These traits are typical of *r*-selected species, which prioritize rapid reproduction and colonization in response to disturbance (MacArthur & Wilson 1967). While this strategy may enhance biodiversity by creating opportunities for other species to establish (Baumane et al. 2025), it also increases the risk of nitrophilous species invasion, particularly in nutrient-enriched environments, as it is probably already the case in Villiers, supplied with high nitrate concentrated groundwater.

4.2 Environmental Drivers of Vegetation Dynamics

The observed phenotypic strategies in *C. mariscus* are closely linked to environmental gradients, particularly moisture and nutrient availability, as reflected by the *CWMs* calculated on vegetation. Two sites with a high *CWM-H* and a low *CWM-N* (e.g., Sacy and Souche), favor the competitive strategy, while Villiers, subject to opposite *CWMs,* promote the colonizer strategy. Marchiennes, however provide an intermediate case, with morphological and reproductive traits of *C. mariscus* reflecting more a colonizer strategy, but a vegetation on the site like the less disturbed sites. The results in Marchiennes could be explained by a legacy effect of past agricultural activities (Peralta et al. 2017) and a recent colonization of open waters by *C. mariscus* rafts (Namura-Ochalska 2005), undergoing less disturbances than Villiers, but still not reaching the dense facies observed in Sacy and Souche, since it develops more towards a *Thelypterido palustris - Phragmitetum australis* vegetation than a *Cladietum marisci* vegetation (Lecocq et al. 2024). Therefore, according to vegetation observations, nutrient concentration of groundwater, and

water levels, it seems that the conditions for *Cladietum marisci* development are only met in Sacy and Souche, with intermediate fluctuating water levels and nutrient loads.

These findings align with previous studies on wetland species, which have demonstrated the critical role of hydrological regimes and nutrient loads in shaping plant community structure (McBride et al. 2011; Namura-Ochalska 2005), phenotypic expression (Richards & Olivas 2020) or competition (Holden & Cahill 2024).

The influence of management practices is also evident in the vegetation dynamics observed across sites. Rotational mowing in Villiers, for example, appears to maintain a balance between *C. mariscus* dominance and species richness by preventing the accumulation of thick litter layers and promoting flowering (Hájková et al. 2022). However, this practice may also facilitate the establishment of nitrophilous species, particularly if nutrient inputs are not adequately controlled (Goodwillie et al. 2020; Hájková et al. 2022). In Villiers, the constant water levels and the regular mowing exporting nutrient allows a development of another vegetation towards *Hydrocotylo vulgaris - Schoenenion nigricantis*. In contrast, the absence of management in Sacy and Souche has led to the development of dense, mature stands with high conservation value but lower species richness (Berquer 2024a).

4.3 Implications for Wetland Management and Conservation

The findings of this study have important implications for the management and conservation of alkaline fens. For dense *C. mariscus* stands, minimal intervention may be the most effective strategy, as these sites already exhibit high conservation status. However, monitoring water table depth is critical to prevent peat mineralization and maintain the hydrological conditions necessary for *C. mariscus* dominance (Conway 1936; Namura-Ochalska 2005). Disturbances of the ecosystem like drought and eutrophication could be monitored at a site level with vegetation relevés (Glanville et al. 2023), but this monitoring seems unable to detect a significant variation during the time span of the study. Therefore, species assemblages at each site are likely driven by legacy effect, and almost not evolve while facing recent changes in the ecosystem, as shown for less than a decade. Completing vegetation releves with real environmental parameters like water levels or the nutrient content of the aquifer supplying the sites appears therefore more informative, since values out of ecological range of the target vegetation can be detected before a potential degradation of the habitat towards a vegetation change. With values monitored around or over thresholds (Grootjans et al. 2021; Kimberly et al. 2013), the managers can anticipate and calibrate conservation actions for alkaline fen vegetations.

In disturbed sites, adaptive management practices such as controlled mowing and nutrient removal can help balance biodiversity conservation with habitat restoration goals (Middleton et al. 2009). However, excessive disturbance should be avoided, as it may shift the community towards a dominance of nitrophilous species and reduce the conservation value of the habitat (Berquer 2024a), as well as for the biodiversity the habitat hosts with sometimes threatened species (Gazaix et al. 2025). Although this observation could plead in favour of the intermediate disturbance hypothesis (Connell 1978), suggesting an increased plant diversity with intermediate disturbance, it does not conclude about a long-term preservation of the habitat, as demonstrated by dense and optimal *C. mariscus* habitat in undisturbed sites. Restoring hydrological regimes

and reducing nutrient inputs are essential to prevent the degradation of alkaline fens into *Phragmites*-dominated or eutrophic systems (Berquer et al. 2024b; Lamers et al. 2015).

4.4 Limitations and Future Research Directions

While this study provides valuable insights into the phenotypic plasticity and vegetation dynamics of *C. mariscus*, several limitations should be acknowledged. First, the study was conducted over a relatively short timeframe for *Cladium mariscus* monitoring (three years), and a longer-term monitoring would be necessary to fully understand the trajectories of phenotypic changes and community composition. Second, genetic analyses were not performed, limiting our ability to distinguish between phenotypic plasticity and attested genetic differentiation among populations. Future research should incorporate genetic studies to confirm the role of clonal vs. sexual reproduction in shaping *C. mariscus* populations. Finally, quantifying peat accumulation and carbon storage in dense *C. mariscus* stands could offer valuable insights into the climate mitigation potential of these ecosystems.

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5. Conclusion

This study demonstrates the critical role of phenotypic plasticity in *Cladium mariscus* for the resilience and conservation of alkaline fens. The two phenotypic strategies—competitive and colonizer—reflect trade-offs between survival and reproduction, shaped by environmental conditions and management practices. For effective conservation, managers must tailor strategies to the specific dynamics of each site, balancing the preservation of dense, mature stands with the need for disturbance to maintain biodiversity.

The findings also highlight the importance of adaptive management in the face of climate change and eutrophication. By integrating phenotypic, community, and environmental data, this study provides a foundation for developing science-based conservation strategies that support the long-term viability of alkaline fens and the species they harbor. Future research should build on these results by incorporating genetic analyses and long-term monitoring to further elucidate the mechanisms underlying phenotypic plasticity and vegetation dynamics in wetland ecosystems.

References

- Agrawal AA **(**2007) Macroevolution of plant defense strategies. Trends ecol evol 22:103-109. https://doi.org/10.1016/j.tree.2006.10.012
- Apori SO, McMillan S, Giltrap M, Tian F (2022) Mapping the restoration of degraded peatland as a research area: a scientometric review. Front Environ Sci 10, https://doi.org/10.3389/fenvs.2022.942788

- Bartoń K (2025) *MuMIn: Multi-Model Inference*. R package version 1.48.11, https://CRAN.R-project.org/package=MuMIn
- Baumane M, Baastrup-Spohr L, Sand-Jensen K, Goldberg I, Thorø Martinsen K, Bruun HH (2025) Nutrients, isolation and lack of grazing limit plant diversity in restored wetlands. J appl ecol 62:144–154. https://doi.org/10.1111/1365-2664.14824
- Bensettiti F, Gaudillat V, Haury J (2002) Cahiers d'habitats Natura 2000. Connaissance et gestion des habitats et des espèces d'intérêt communautaire. Tome 3 - Habitats humides. MATE/MAP/MNHN, Paris.
- Berquer A (2024) Modalités du pâturage en tourbières. Quelles cibles, quels obectifs ? In : Franquin et al Faire pâturer les tourbières alcalines : entre gestion conservatoire et impacts, LIFE Anthropofens, Conservatoire d'espaces naturels des Hauts-de-France, 2.1:15-17
- Berquer A, Levrault S, Castelli M, Alderweireld F, André A, Antoine P, Brasseur B, Capoulade J, Czerniak L, Décultot C, François R, Garcia C, Hummel J, Janczak A, Meire G, Opdekamp W,Trongneux P, Vandendriessche M, Chombart C, Daubresse R, James M, Duran P (2024) Fonctionnement des tourbières alcalines, gestion de l'eau et restauration. LIFE Anthropofens, Conservatoire d'espaces naturels des Hauts-de-France, Boves. 52p
- Bruelheide H, Dengler J, Purschke O et al (2018*)* Global trait–environment relationships of plant communities. Nat ecol evol 2:1906–1917. https://doi.org/10.1038/s41559-018-0699-8
- Cahill JF, McNickle GG, Lamb EG **(**2010) Plants integrate information about nutrients and neighbors. Science 328:1652–1654. https://doi.org/10.1126/science.1189736
- Callaway RM, Brooker RW, Choler P, Kikvidze Z, Lortie CJ, Michalet R, Paolini L, Pugnaire FI, Newingham B, Aschehoug ET, Armas C, Kikodze D, Cook BJ (2002). Positive interactions among alpine plants increase with stress. Nature 417:844–848. https://doi.org/10.1038/nature00812
- Caron N, Gaudin G, Leglise L (2020) Les marais de la Souche: plan de gestion multi-sites 2021-2030. Conservatoire d'espaces naturels des Hauts-de-France, 381 p
- Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199:1302–1310. https://doi.org/10.1126/science.199.4335.1302
- Conway VM (1936) Studies in the autecology of *Cladium mariscus* R.BR. New phytol 35:359-380. https://doi.org/10.1111/j.1469-8137.1936.tb06888.x
- Coulombel R (2020) Grille d'évaluation de l'état de conservation des "Marais calcaires à *Cladium mariscus* et espèces du *Caricion davallianae*" (7210). Guide d'évaluation à l'échelle des sites Natura 2000. Conservatoire Botanique National de Bailleul.
- Decodts H, Pencoat-Jones A (2020) Plan de gestion 2021-2030 Propriétés départementales des marais de Sacy. Conservatoire d'espaces naturels des Hauts-de-France.
- Díaz S, Kattge J, Cornelissen JHC et al. (2016) The global spectrum of plant form and function. Nature 529:167–171. https://doi.org/10.1038/nature16489
- Fourmy F, Janczak A, Rousseaux L (2022) Marais de Villiers, plan de gestion 2023-2027. Conservatoire d'espaces naturels des Hauts-de-France, 210p
- Gallego-Sala A, Charman D, Brewer S, Page S, Prentice C et al. (2018) Latitudinal limits to the predicted increase of the peatland carbon sink with warming. Nat clim change 8(10):907-913. https://doi.org/10.1038/s41558-018-0271-1
- Gazaix A, Rendell C, Berquer A, Caron N, Besnard A, Couturier T (2025) Occupancy changes over the summer of the rare fen raft spider *Dolomedes plantarius* in a drained fen

strongly depend on vegetation structure. Insect conserv divers 1–11. https://doi.org/10.1111/icad.70048

- Ghalambor CK, McKay JK, Carroll SP, Reznick DN (2007) Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. Funct ecol 21:394-407. https://doi.org/10.1111/j.1365-2435.2007.01283.x
- Gianoli E, Palacio-López K (2009) Phenotypic integration may constrain phenotypic plasticity in plants. Oikos 118: 1924–1928. https://doi.org/10.1111/j.1600-0706.2009.17884.x
- Glanville K, Sheldon F, Butler D, Capon S (2023) Effects and significance of groundwater for vegetation: A systematic review. Sci total environ 875: 162577. https://doi.org/10.1016/j.scitotenv.2023.162577
- Goodwillie C, McCoy MW, Peralta AL (2020) Long-term nutrient enrichment, mowing, and ditch drainage interact in the dynamics of a wetland plant community. Ecosphere 11(10):e03252. https://doi.org/10.1002/ecs2.3252
- Grootjans AP, Wolejko L, de Mars H, Smolders AJ, van Dijk G (2021) On the hydrological relationship between Petrifying-springs, Alkaline-fens, and Calcareous-spring-mires in the lowlands of North-West and Central Europe; consequences for restoration. Mires Peat 27: 1–18 https://doi.org/10.19189/MaP.2020.OMB.StA.2134
- Hájková P, Horsáková V, Peterka T, Janeček Š, Galvánek D, Dítě D, Horník J, Horsák M, Hájek M (2022) Conservation and restoration of Central European fens by mowing: A consensus from 20 years of experimental work. Sci total environ 838:156045. https://doi.org/10.1016/j.scitotenv.2022.157293
- Hinzke T, Tanneberger F, Aggenbach C et al. (2022) Response patterns of pen pedges to a nutrient gradient indicate both geographic origin-specific genotypic differences and phenotypic plasticity. Wetlands 42:113 https://doi.org/10.1007/s13157-022-01629-4
- Holden EM, Cahill Jr JF (2024) Plant trait dissimilarity increases competitive interactions among co-occurring plants. Funct ecol, 28:1464-1474. https://doi.org/10.1111/1365-2435.14561
- Joosten H, Tapio-Biström ML, Tol S (2012) Peatlands – guidance for climate change mitigation through conservation, rehabilitation and sustainable use. Mitigation of climate change in agriculture series 5, Second edition.
- Kimberley S, Coxon C, Craig M, Schutten J (2013) Determination of nutrient threshold values relevant to groundwater dependant terrestrial ecosystems (GWDTEs) in Ireland: Progress and challenges. Meeting of the hydrogeological group of the geological society, Birmingham and Midland Institute, Birmingham UK.
- Kraft NJB, Adler PB, Godoy O, James EC, Fuller S, Levine JM (2015) Community assembly, coexistence and the environmental filtering metaphor. Funct Ecol 29:592-599. https://doi.org/10.1111/1365-2435.12345
- Kreyling J, Zeterberg K, Aggenbach K et al (2025) Paludiculture maintains peat formation potential in rewetted temperate fens. Agron sustain dev 45:67. https://doi.org/10.1007/s13593-025-01062-x
- Kunstler G, Falster D, Coomes D et al (2016) Plant functional traits have globally consistent effects on competition. Nature 529:204–207. https://doi.org/10.1038/nature16476
- Lamers LPM, Vile MA, Grootjans AP et al (2015*)* Ecological restoration of rich fens in Europe and North America: from trial and error to an evidence-based approach. Biol rev 90(1):182–203. https://doi.org/10.1111/brv.12102

- Landolt E (1977) Ökologische Zeigerwerte zur Schweizer Flora. Stiftung Rübel, Zürich.
- Laughlin DC, Gremer JR, Adler PB, Mitchell RM, Moore MM (2020) The Net Effect of Functional Traits on Fitness, Trends ecol evol 35(11):1037-1047. https://doi.org/10.1016/j.tree.2020.07.010 .
- Lavorel S, Grigulis K, McIntyre S, Williams NSG, Garden D, Dorrough J, Berman S, Quétier F, Thébault A, Bonis A. (2008) Assessing functional diversity in the field – methodology matters! Funct ecol, 22:134-147. https://doi.org/10.1111/j.1365-2435.2007.01339.x
- Lecocq V, Savary J, Gallet B (2024) Plan de gestion 2024-2028 de la RNN de la Tourbière alcaline de Marchiennes (Marchiennes, 59). Conservatoire d'espaces naturels des Hauts-de-France, Boves. 194 p
- Leifeld J, Menichetti L (2018) The underappreciated potential of peatlands in global climate change mitigation strategies. Nat commun 9:1071 https://doi.org/10.1038/s41467-018-03406-6
- Limpens J, Berendse F, Blodau C, Canadell JG, Freeman C, Holden J, Roulet N, Rydin H, Schaepman-Strub G (2008) Peatlands and the carbon cycle: from local processes to global implications – a synthesis. Biogeosciences 5:1475-1491. https://doi.org/10.5194/bg-5-1475-2008
- Loisel J, Yu Z, Beilman DW, Camill P, Alm J et al. (2014) A database and synthesis of northern peatland soil properties and Holocene carbon and nitrogen accumulation. Holocene 24(9):1028-1042. https://doi.org/10.1177/0959683614538073
- MacArthur RH, Wilson EO (1967) The Theory of Island Biogeography. Princeton University Press, Princeton, NJ.
- Martens HR, Laage K, Drexler A, Heinsohn V, Wegner N, Muster C, Diekmann M, Seeber E, Kreyling J, Michalik P, Tanneberger F (2023) Paludiculture can support biodiversity conservation in rewetted fen peatlands. Sci rep 13:18091 https://doi.org/10.1038/s41598-023-44481-0
- McBride A, Diack I, Droy N, Hamill H, Jones P, Schutten J et al (2011) The fen management handbook. Perth, UK: Scottish Natural Heritage
- Middleton BA, Holsten B, van Diggelen R (2006) Biodiversity management of fens and fen meadows by grazing, cutting and burning. Appl veg sci 9:307-316. https://doi.org/10.1111/j.1654-109X.2006.tb00680.x
- Minayeva TY, Bragg O, Sirin AA (2017) Towards ecosystem-based restoration of peatland biodiversity. Mires Peat 19(1):1-36. https://doi.org/10.19189/MaP.2013.OMB.150
- Mueller-Dombois D, Ellenberg H. (1974) Aims and Methods of Vegetation Ecology. John Wiley & Sons, New York.
- Namura-Ochalska A (2005) Contribution to the characteristic of *Cladium mariscus* (L.) Pohl population in the initial zone of floating mat on an oligo-humotrophic lake in north-eastern Poland. Acta soc bot pol. 74:167-173. https://doi.org/10.5586/asbp.2005.022
- Nicotra AB, Atkin OK, Bonser SP et al (2010) Plant phenotypic plasticity in a changing climate Trends plat sci 15(12):684–692. https://doi.org/10.1016/j.tplants.2010.09.008
- Nilsson K (2016) Alkaline fens valuable wetlands but difficult to manage. TemaNord 2016:515
- Peralta AL, Muscarella ME, Matthews JW (2017) Wetland management strategies lead to tradeoffs in ecological structure and function. Elementa: sci anthropocene 5:74. https://doi.org/10.1525/elementa.253

- Pierik R, Mommer L, Voesenek LACJ (2013) Molecular mechanisms of plant competition: neighbour detection and response strategies. Funct Ecol 27:841–853. https://doi.org/10.1111/1365-2435.12010
- R Core Team (2025) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria
- Richards CL, Bossdorf O, Muth NZ, Gurevitch J, Pigliucci M (2006) Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. Ecol lett 9(8):981–993. https://doi.org/10.1111/j.1461-0248.2006.00950.x
- Richards JH, Olivas PC (2020) A common-mesocosm experiment recreates sawgrass (*Cladium jamaicense*) phenotypes from Everglades marl prairies and peat marshes. Am j bot 107(1): 56–65. https://doi.org/10.1002/ajb2.1411
- Schmitt J, McCormac AC, Smith H (1995) A test of the adaptive plasticity hypothesis using transgenic and mutant plants disabled in phytochrome-mediated elongation responses to neighbors. Am nat 146:953–969. https://doi.org/10.1086/285832
- Seer FK, Schrautzer J (2014) Status, future prospects, and management recommendations for alkaline fens in an agricultural landscape: a comprehensive survey. J nat conserve 2(4):358-368 https://doi.org/10.1016/j.jnc.2014.03.003
- Sobral M (2021) All traits are functional: an evolutionary viewpoint. Trends plant sci 26(7) :674-676. https://doi.org/10.1016/j.tplants.2021.04.004
- Tanneberger F, Tegetmeyer C, Busse S et al (2017*)* The peatland map of Europe. Mires peat 19(22):1–17. https://doi.org/10.19189/MaP.2016.OMB.264
- Valladares F, Gianoli E, Gómez JM (2007) Ecological limits to plant phenotypic plasticity. New phytol 176: 749-763. https://doi.org/10.1111/j.1469-8137.2007.02275.x
- Violle C, Navas ML, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007) Let the concept of trait be functional! Oikos 116:882-892. https://doi.org/10.1111/j.0030-1299.2007.15559.x
- Weiner J (2004) Allocation, plasticity and allometry in plants. Perspect plant ecol evol syst 6:207–215. https://doi.org/10.1078/1433-8319-00083
- Wickham H (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York. https://ggplot2.tidyverse.org
- Winckel A, Ollagnier S, Gabillard S (2022) Managing groundwater resources using a national reference database: the French ADES concept. SN Appl Sci 4, 217. https://doi.org/10.1007/s42452-022-05082-0
- Zedler JB, Kercher S (2005) Wetlands resources: status, trends, ecosystem services and restorability. Annu rev environ resour 30:39-74. https://doi.org/10.1146/annurev.energy.30.050504.144248
- Zhang B, Hastings A, Grosholz ED, Zhai L (2023) The comparison of dispersal rate between invasive and native species varied by plant life form and functional traits. Mov Ecol 11:73. https://doi.org/10.1186/s40462-023-00424-y

Statements & Declarations

Funding

This work was funded by the LIFE programme, under grant number LIFE18NAT/FR/000906, including funding from the European Commission, the French waterboards Agence de l'Eau Artois-Picardie and Agence de l'Eau Seine-Normandie.

Competing Interests

The authors have no relevant financial or non-financial interests to disclose

Author contributions

AB contributed to conceptualization, data acquisition and management, formal analysis and wrote the first draft of the manuscript. RC conceptualized and discussed the conservation state of vegetation. Both authors commented each version, read and approved the final manuscript.

Data Availability

The datasets generated and analysed during the current study are available from the corresponding author upon request.

Figures and Tables

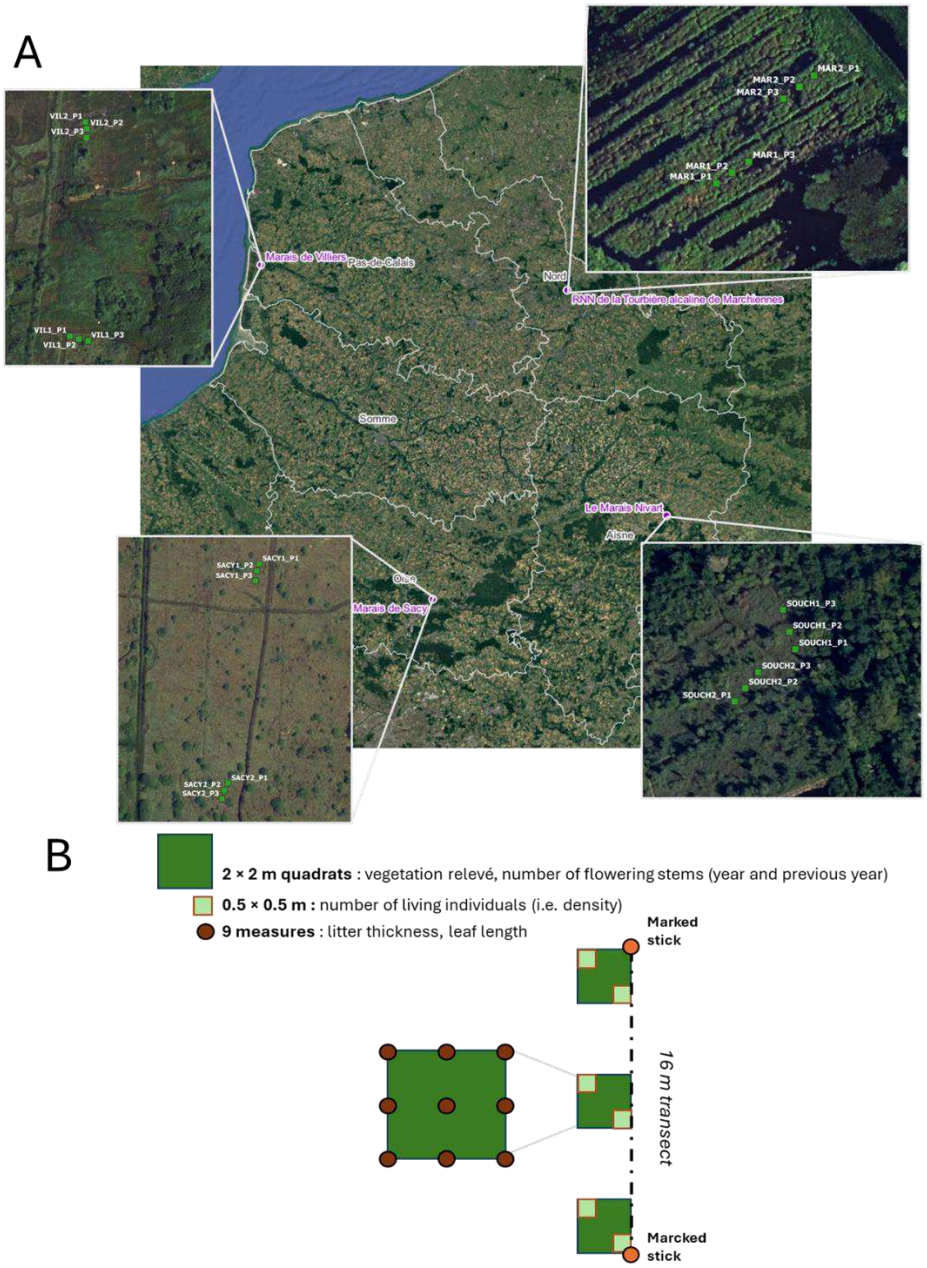

Figure 1: Location of the study sites in Northern France (A) and schematic representation of the sampling design (B). Each session and site consists of two randomly placed transects within the *Cladium*-dominated vegetation. Along each transect, three 4m² quadrats were systematically sampled to monitor morphological, reproductive and environmental variables

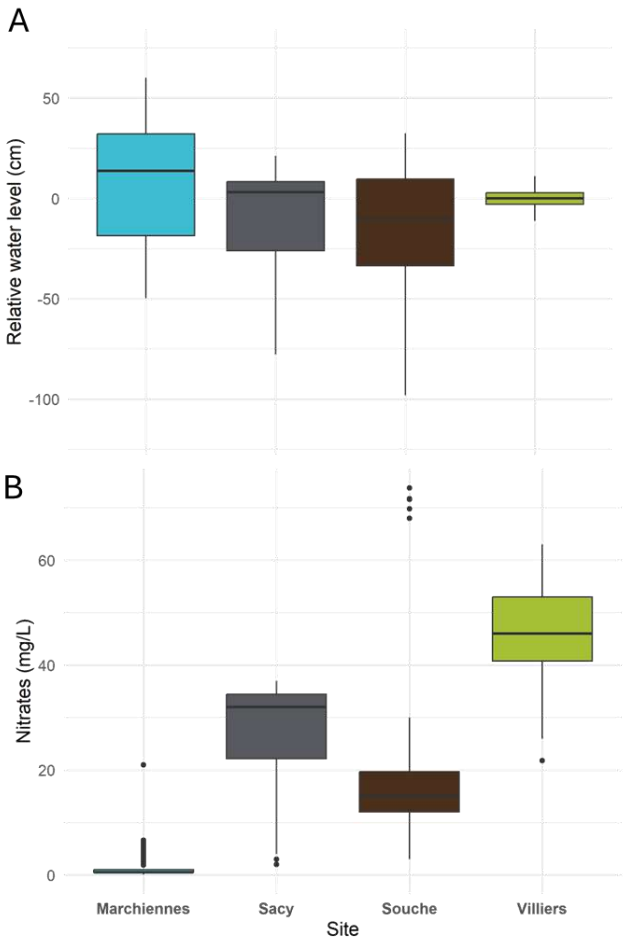

Figure 2: Representation of the water levels relative to the soil surface (A) and nitrate concentrations of the groundwater supplying each site (B). Sites have significant differences for both variables.

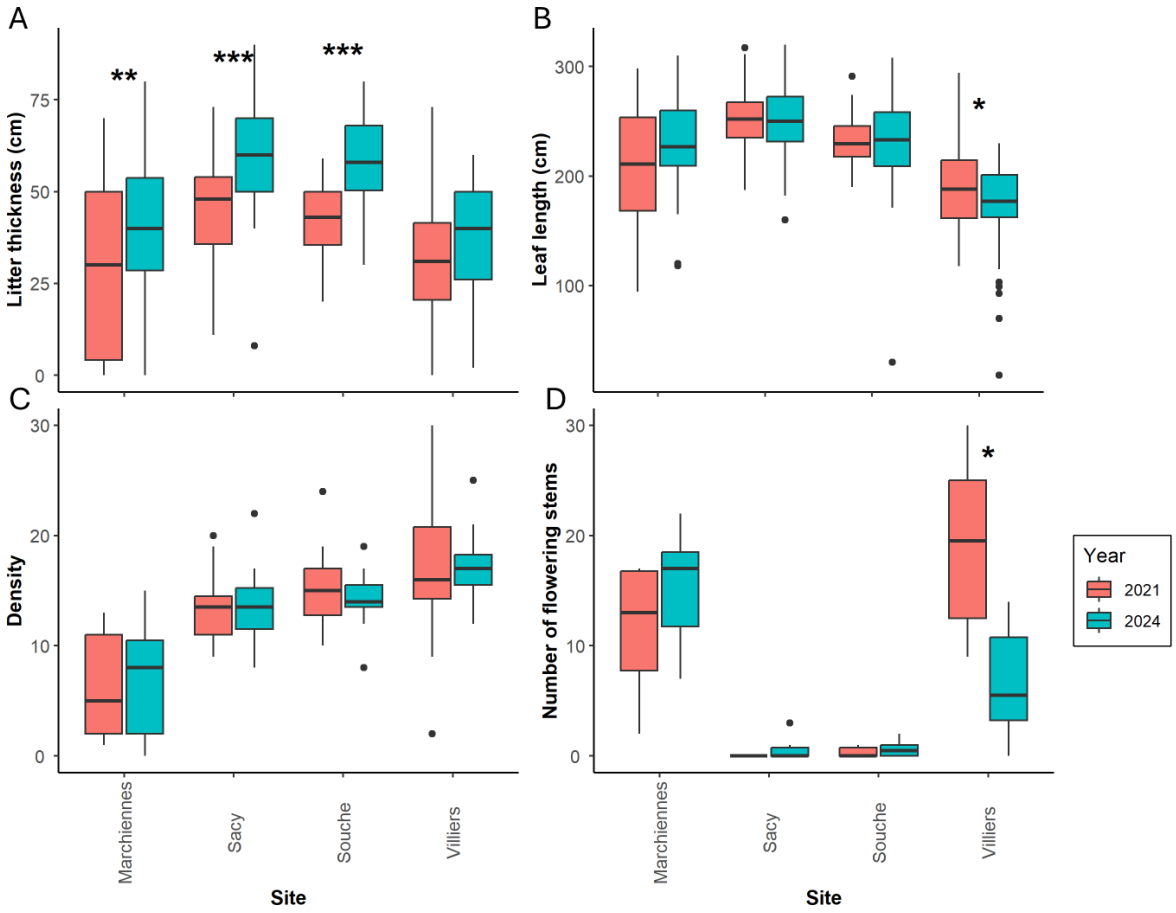

Figure 3: Spatial and temporal variation in morphological traits of *Cladium mariscus* across four alkaline fen sites in Northern France. Boxplots show the distribution of (A) litter thickness (cm), (B) leaf length (cm), (C) stem density (stems m^{-2}), and (D) number of flowering stems (stems m^{-2}) in 2021 (red) and 2024 (blue). Statistical comparisons between years were performed using paired t-tests, with significance levels indicated as follows: *p < 0.05; **p < 0.01; ***p < 0.001. Boxes represent interquartile ranges (IQR), horizontal lines indicate medians, whiskers extend to 1.5 × IQR, and dots show outliers.

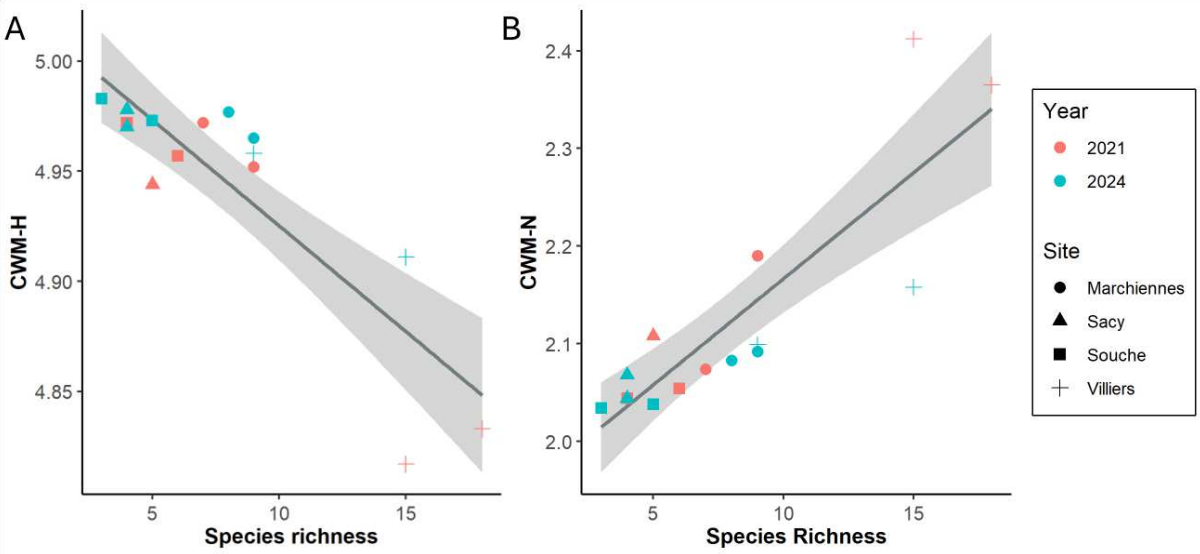

Figure 4: Linear regressions of the moisture *CWM-H* (A) and trophic *CWM-N* (B) indices according to species richness reported on each transect. Both models are significant.

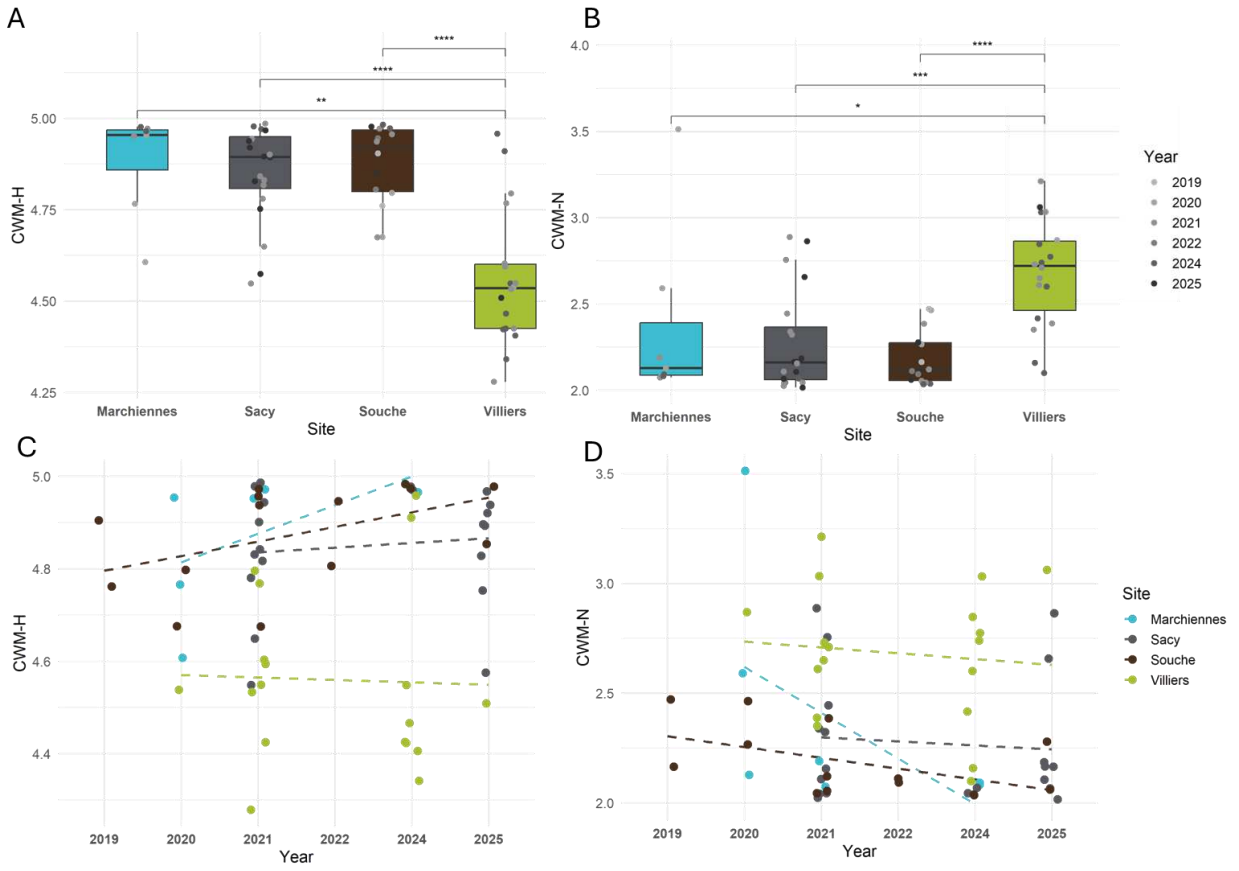

Figure 5: Site comparisons (A, B), and evolution (C, D) of the community weighted means of vegetation moisture (A, C) and trophic (B, D) indices calculated on 58 vegetation relevés. Villiers is the only site showing significant differences with the other ones, whereas both indices do not show any significant relationship with the time. * : $p < 0.05$, ** : $p < 0.01$, *** : $p < 0.001$, **** : $p < 0.0001$, with Wilcoxon rank test. Dashed lines of linear models indicate no significant relationships.

Table 1: Results of a Dunn post-hoc test for water levels and nitrate concentrations of groundwater between sites, after significant Kruskal-Wallis tests for water levels ($\chi^2 = 10610$, df = 3, $p < 0.0001$) and nitrates ($\chi^2 = 294.4$, df = 3, $p < 0.0001$)

	Comparison	Z	p
Water levels	Marchiennes-Sacy	-66.01	**< 0.001**
	Marchiennes – Souche	-209.14	**< 0.001**
	Sacy – Souche	-129.00	**< 0.001**
	Marchiennes – Villiers	78.50	**< 0.001**
	Sacy – Villiers	146.84	**< 0.001**
	Souche – Villiers	317.83	**< 0.001**
Nitrate concentration	Marchiennes-Sacy	-9.13	**< 0.001**
	Marchiennes – Souche	-8.91	**< 0.001**
	Sacy – Souche	1.94	0.31
	Marchiennes – Villiers	-16.65	**< 0.001**
	Sacy – Villiers	-4.33	**< 0.001**
	Souche – Villiers	-7.55	**< 0.001**

567 Table 2: Pairwise comparisons with paired t-tests between sites for four variables: Litter
568 thickness, Leaf length, Density and the Number of flowering stems

	Litter thickness			Leaf length			Density			Number of flowering stems		
	t	df	p	t	df	p	t	df	p	t	df	p
Marchiennes-Sacy	-6.87	194	**< 0.001**	-5.92	192	**< 0.001**	-5.08	33.3	**< 0.001**	7.45	11.5	**< 0.001**
Marchiennes – Souche	-6.03	177	**< 0.001**	-2.06	204	**0.040**	- 6.02	31.9	**< 0.001**	7.38	11.3	**< 0.001**
Marchiennes – Villiers	-0.12	195	0.903	6.68	224	**< 0.001**	- 6.22	42.0	**< 0.001**	0.155	18.8	0.878
Sacy – Souche	1.48	209	0.141	4.77	236	**< 0.001**	-1.13	45.8	0.262	-0.518	20.5	0.61
Sacy – Villiers	8.16	214	**< 0.001**	14.9	220	**< 0.001**	-2.49	37.3	**0.017**	-4.63	11.2	**< 0.001**
Souche – Villiers	7.30	208	**< 0.001**	10.3	230	**< 0.001**	-1.73	35.9	0.093	-4.59	11.1	**< 0.001**

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Supplementary

Supplementary table 1: Description of the piezometers used for groundwater nitrate concentrations estimations, with location, code, the time and number of samplings and the monitored aquifere. The code of each piezometer provides the access to the data on ADES Database.

Site	Code in ADES	Start sampling	End sampling	Number of samplings	Name of the aquifere
Marchiennes	BSS000CFNN	2008/08/20	2023/09/14	13	Paris basin Thanetian sands
	BSS000CEQS	1984/11/29	2024/04/15	25	Senonian-Turonian chalk
	BSS000CBYN	1993/12/11	2023/11/02	71	
Sacy	BSS000GZFU	1996/06/14	2024/04/23	17	Senonian-Turonian chalk
	BSS000GYXL	1998/08/25	2023/09/27	8	
	BSS000GZFV	1996/01/19	2023/02/15	17	
Souche	BSS000FXBB	2015/11/03	2024/04/11	4	Senonian-Turonian chalk
	BSS000FWYD	2005/06/22	2013/03/22	5	
	BSS000FWZF	1998/04/28	2024/07/10	86	
Villiers	BSS000BPVD	1974/09/08	2016/02/04	83	Senonian-Turonian chalk

Supplementary table 2 : Model selection performed for *CWM-H* and *CWM-N* according to morphologic and community variables. “Mean” and “SD” indicate respectively the mean and standard deviation measured for each variable. Some variables were not included due to strong correlations. Each variable was scaled prior analysis. Only the models with a difference from the best model AIC less than 2.0 are presented.

	Variables								model		
	Mean litter	SD litter	Mean Stem Height	Mean Leaf length	SD Leaf length	Density	Mean stem density	Richness	df	AIC	Delta
CWM-H				-		-	-	-	6	19.4	0.00
				-		-		-	5	19.9	0.49
				-	+	-		-	6	20.0	0.57
				-	+	-	-	-	7	20.1	0.76
					+	-		-	5	20.4	1.01
		+		-		-		-	6	20.8	1.38
		+		-		-	-	-	7	20.8	1.39
	+			-		-	-	-	7	20.8	1.45
		+		-	+	-		-	7	20.9	1.47
		+			+			-	5	20.9	1.51
	+				+	-		-	6	20.9	1.54
		+			+	-		-	6	21.0	1.63
	+			-		-		-	6	21.2	1.85
	+	+			+			-	6	21.3	1.90
			+	-		-	-	-	7	21.3	1.92
CWM-N					-			+	4	27.2	0.00
				+		+	+	+	6	27.8	0.57
								+	3	27.8	00.59
						+	+	+	5	28.5	1.37
						+		+	4	28.7	1.47
				+		+		+	5	28.7	1.52
			-					+	4	28.7	1.57
					-	+		+	5	28.8	1.57
					-	+	+	+	6	29.0	1.80
	+				-			+	5	29.0	1.82
					-		+	+	5	29.0	1.83
		-			-			+	5	29.0	1.84
	-			+		+	+	+	7	29.0	1.87
			-		-			+	5	29.1	1.88
				+	-			+	5	29.1	1.95
		+						+	4	29.1	1.96