The ecology of diatoms in peatlands:

Communities from Tierra del Fuego peat bogs as a study case

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Abstract

Peatlands are one of the most widespread wetland types in the world, inhabited by a remarkable diversity of diatom species. The first part of this chapter overviews the main characteristics of diatom communities from peatlands on a global scale, the key genera, their ecological aspects, and the adaptations to these particular environments. The second part focuses on a study case of diatom communities from Tierra del Fuego-Argentina, the southernmost extensive peatland area in the world. Two dome-shaped peat bogs were studied: Rancho Hambre and Valle de Andorra, which host several shallow ponds in a *Sphagnum magellanicum* matrix. In order to survey their diatom assemblages and their relationship with the environmental parameters at different scales, diatom communities were compared to those of peripheral limnetic environments (moats; rivers; beaver dams), within peat bog environments (ponds *vs.* moss matrix), as well as within pond habitats (sediments *vs.* periphyton). Despite being 50 km apart, both peat bogs showed highly similar species compositions. Furthermore, peat bog assemblages were unique and stood up from their surroundings. A high species turnover was observed despite the short distance between peat bogs and their peripheral environments, mainly due to environmental filters imposed by distinct physical and chemical conditions. The most relevant parameters in this sense were pH, total hardness, total phosphorus and conductivity. Ponds were the most species-rich environments, while only a few species inhabited the *Sphagnum* matrix. Within ponds, periphyton on different mosses (*Sphagnum magellanicum*, *Sphagnum fimbriatum*, *Sanionia uncinata*) showed similar species composition and low richness. On the other hand, the benthos was the richest community, with a high percentage of exclusive species. We therefore conclude that the sediment hosts the most representative diatom assemblages of peat bogs, and recommend sampling benthos whenever studying diatom biodiversity in these environments.

Keywords: Bacillariophyceae; moss; ponds; *Sphagnum*; diatom communities; wetlands; biodiversity.

1.1 Introduction:

1.1.1 Wetlands and Peatlands: general characteristics and global significance

In the last decades, there has been an increasing interest in studies in wetland ecology, mainly because of their unique biodiversity, their primordial role as water reservoirs and their positive impact on human welfare (food/materials suppliers) in general. Wetlands provide approximately 40% of all Nature's contribution to mankind [1.19]. Nevertheless, they also rank amongst the most vulnerable environments worldwide. The main threats they face include dramatic changes in land use, mainly due to increasing urbanization and uncontrolled expansion of agriculture/livestock lands, pollution and overexploitation of their resources [1.25, 1.46]. As discussed in Quintana & Mataloni [1.80], the definition of wetlands is broad and has varied with time and authors. Nonetheless, wetlands can be summarized as a diverse set of ecosystems with standing water or waterlogged, anoxic soils, together with plant and animal species adapted to these environmental conditions. The hydrological cycle defines the structural and functional characteristics of these environments.

One-third of all wetlands worldwide are peatlands, an ecosystem type present in at least 180 countries and representing 3% of the total land surface [1.2, 1.76]. Peatlands occur under particular environmental

Peatlands are established in areas where water can accumulate due to a positive precipitation/evaporation balance, which explains their predominance in cold (boreal and sub-Arctic) and humid (oceanic and humid tropical) regions [1.25, 1.47] and their higher frequency in the Northern compared to the Southern Hemisphere. From a climate regulation point of view, peatlands play a crucial role on a global scale, as they are involved in the worldwide greenhouse gas balance [1.45]. Peatlands also act as global water reservoirs (10% of the freshwater) able to buffer longer periods of drought but also to absorb large quantities of water during heavy rainfall or flooding [1.47, 1.62]. Nevertheless, these balances heavily depend on the ecosystem health. Degraded peatland stops sequestering CO_2 from the atmosphere and the accumulated peat begins to decompose aerobically, releasing massive amounts of carbon into the system. The large amounts of historically sequestered carbon can be released because of degradation through drainage, excavation or fertilization [1.5].

1.1.2 Peatland classification and environmental characterization.

A peatland area encompassing potentially peat-forming vegetation is commonly named mire. Mires can be classified into two types based on their water source [1.63]: Minerotrophic fens are flat or depressed systems fed by groundwater or surface water flows, while ombrotrophic bogs are isolated from groundwater influence, and thus water and nutrient supply exclusively depend on direct precipitation [1.86]. Peat accumulation in ombrotrophic bogs results in the development of a domed-shaped morphology (known as raised bogs), frequently showing a *Sphagnum* mosses-dominated vegetation [1.84]. Peat-forming vegetation starts to develop at the edges of water bodies and gradually the entire basin gets filled with peat, eventually resulting in the transformation of the lentic habitat into a more terrestrial system. Once the mire basin is entirely filled with peat, *Sphagnum* mosses can generate small hummocks above the groundwater table, and grow eventually into elevated domes isolated from groundwater influence. Such mires are commonly known as transition mires [1.63], and display a mosaic of minerotrophic, semi-ombrotrophic, and ombrotrophic environmental conditions.

In general, mires with different hydrological regimes display distinct pH and nutrient conditions. The transition from minerotrophic fens to ombrotrophic bogs causes a progressive decrease in pH, ranging from circumneutral to acidic conditions, consequently decreasing nutrient availability in distrophic bogs [1.25]. *Sphagnum* mosses play a key role in this environmental transition as they efficiently remove cations liberating protons [1.18] and thus creating more acidic conditions in ombrotrophic mires.

The complex topography of peatland landscapes generally results in the development of a mosaic of different environments [1.38]. This environmental diversity can be observed at several spatial scales. For example, in Rancho Hambre peat bog, a gradual decrease in pH and increase in conductivity was observed over short distances (3.2 m) along a terrestrialization gradient from open water of ponds to the drier surrounding mosses [1.9, 1.68]. Furthermore, the microtopography-determined hydrological network increases habitat complexity even in small areas, with ponds only meters apart displaying very different chemical features [1.36].

From a biodiversity point of view, peatlands are considered to be important hotspots because they support a high number of specialized organisms that can cope with many inimical conditions such as low pH values and dystrophy [1.34, 1.43,1.44, 1.81, 1.86]. Nutrient-poor peat bogs are essential ecosystems maintaining and protecting the biodiversity of microalgae sensitive to eutrophication [1.20].

1.2 Singularity of peatland diatoms

1.2.1 Main genera and species in peatlands

Among autotrophs, diatoms (Bacillariophyceae) and desmids (Desmidiaceae) represent some of the richest taxonomic groups, with a high number of taxa restricted to these habitats [1.9, 1.14, 1.20, 1.57, 1.68, 1.73, 1.74].

The presence and diversity of these algal groups in peatlands are highly controlled by pH, conductivity, nutrient availability, water availability, and water table depth, selecting acidophilous, halophobic, aerophilic and oligotrophic taxa [1.8, 1.67, 1.75, 1.92]. Peatland diatom communities are dominated by a handful of genera, among which *Eunotia* and *Pinnularia* are the most species-rich [1.14, 1.25, 1.78, 1.79]. Most *Eunotia* species present narrow ecological preferences and are typically observed in oligotrophic waters, often rich in humic acids and strongly associated with *Sphagnum* spp. in peat bogs or related habitats [1.61]. *Pinnularia*, in turn, is a large genus comprising more than 1800 species that can be found in a variety of habitats, many of which are indicative of acidic and oligotrophic freshwaters [1.53]. Several other genera, such as *Frustulia, Neidium, Brachysira, Kobayasiella* and *Encyonema*, are also frequently recorded in oligotrophic, acidic habitats and represent therefore an important part of peatland diatom communities [1.52, 1.59, 1.60].

Some of the most frequently cited species in peatlands include *Eunotia sphagnicola* Van de Vijver, A.Mertens & Lange-Bert.(often erroneously reported as *E. paludosa* Grunow, see below), *Eunotia seminulum* Nörpel-Schempp & Lange-Bert., *Eunotia exigua* (Bréb. *ex* Kütz.) Rabenh., *Pinnularia borealis* Ehrenb., *Pinnularia microstauron* (Ehrenb.) Cleve, *Pinnularia viridis* (Nitzsch) Ehrenb., *Tabellaria floculossa* (Roth) Kütz., *Achnanthidium minutissimum* (Kütz.) Czarn., *Frustulia saxonica* Rabenh. and others. Many of these species are considered cosmopolitan, with a wide distribution on a global scale.

However, it is essential to note that diatom diversity and possible local endemism, especially outside Europe and North America, has long been underestimated, primarily due to force–fitting [1.91]. On one hand, this could have led to overestimate the distribution area of iconic species by misidentifying similar locally distributed taxa. On the other, force-fitting could underestimate actual diversity. For instance, a recent study on the type material of *Eunotia paludosa* has shown that our current concept of this species was wrong. The analysis resulted in the description of at least three different species, with similar but distinguishable morphologies, and redefined biogeographies and ecological preferences [1.94]. Also, the combination of morphometric and molecular studies in the *Pinnularia borealis* complex has shown the presence of truly cryptic species [1.77]. Flaws in the identification of diatom species could impair their usefulness as environmental indicators, in paleoenvironmental reconstructions or in biogeographical studies. In this context, there is a pressing need for detailed studies on peatlands diatoms, in order to refine taxonomic and ecological information about well-known but also new, potentially endemic, taxa. The analysis of type material and other historic material is crucial to establish not only the correct taxonomic identity of the species but also their ecological preferences. The recent revision of the European *Brachysira* flora is a clear example of how such studies might be undertaken [1.101, 1.102, 1.94].

1.2.2 Physical, chemical and landscape-scale drivers of diatom communities

Within the physical and chemical variables of freshwater environments, pH is the main factor that influences the establishment and distribution of diatoms since, in general, most species have a relatively narrow pH range [1.3, 1.21, 1.92]). DeNicola [1.21] reviewed diatoms from highly acidic conditions and concluded that only a few taxa are capable of maintaining a viable population below pH 3.5. However, most aquatic environments dominated by *Sphagnum* rarely have pH values below this limit [1.42], which allows them to support a rich diatom flora. The influence of pH and moisture on diatom communities was observed in many peatlands or mossy environments in Europe [1.25, 1.74, 1.78], North America [1.41], South America [1.68], the sub-Antarctic region [1.98] or Oceania [1.50]. The diversity of diatoms in peatlands is usually positively related to the pH values of individual localities [1.73].

A study on diatom communities along a mineral gradient in fens in the Czech Republic and Slovakia demonstrated that water chemistry substantially influenced the spring fen biota [1.25]. These authors found that species richness decreased significantly from mineral-rich to mineral-poor sites, and the structure and composition of diatom assemblages were ruled by a strong environmental gradient of pH, calcium, and conductivity.

At a landscape scale, peatlands encompass a great diversity of habitats and microhabitats. In ombrotrophic peatbogs, the moss matrix frequently encompasses a water bodies ranging from numerous small ponds to less frequent shallow lakes, which show contrasting community compositions. Also, the microtopography of peatland surfaces can have key implications for hydrologic conditions, generating small-scale variations in environmental features that translate into more ecological niches where a greater diversity of microorganisms can establish. Nevertheless, in Tierra del Fuego, Mataloni [1.68] found that microalgal communities were progressively impoverished along sampling transects established from the open water of ponds to the interstitial water among *Sphagnum* mosses ca. 3 m away from the water edge, characterized by a constant decrease in pH and humidity and increase in conductivity.

The moisture of the sampling site strongly depends on the water table depth, and is influenced by its position on the mire surface. Poulíčková et al. [1.78] studied three spring fens from the Czech Republic and Slovakia. They demonstrated that diatom abundance, species richness and diversity decrease with the decreasing moisture in the microsite. *Eunotia paludosa* was highlighted as a typical species of dry hummock tops, accompanied by *Pinnularia rupestris* Hantzsch and *Achnanthes lanceolata* (Bréb. *ex* Kütz.) Grunow. Following these results, Chen et al. [1.15] studied diatom communities from different microhabitats within three montane peatlands in central China. They found that *Luticola* and *Hantzschia*, desiccation-tolerant genera, and *Eunotia paludosa*, *Hantzschia amphioxys* (Ehrenb.) Grunow, *Pinnularia borealis* and *Luticola mutica* (Kütz.) Mann were good indicators for hummocks microhabitats, characterized by moisture-limited and oxidizing conditions. Meanwhile, *Eunotia minor* (Kütz.) Grunow and *Eunotia seminulum* preferred the wetter conditions of the hollows. In addition, other species, such as *Aulacoseira ambigua* (Grunow)

Simonsen or *Neidium ampliatum* (Ehrenb.) Krammer, were good indicators for ditch edges, a hydrologically unstable microhabitat with highly variable environmental conditions wherein diatoms with different life strategies coexisted.

Historically, as it has also occurred in freshwater ecosystems, the planktonic community of the water bodies has received primary attention in most studies; however, the contribution to diversity of other communities such as periphyton or benthos must be emphasized, especially in shallow ponds from peatlands. For example, a recent study on the peatland pools from Czech Republic [1.71] has showed that at the local scale, the community structure of diatoms differed between *Sphagnum* periphyton and epipelon from the ponds. Another source of environmental variation may be the identity of the moss species forming the peat bog. The morphology of the cauloids and phyllodes and the process of cation exchange with the environment can differ between moss species, influencing the growth and development of epiphytic algae [1.22, 1.78].

In sum, in agreement with Gaiser & Rühland [1.32] and Simkhada and Jüttner [1.88], it is important to sample in detail the different habitats, microhabitats or substrates within wetlands, since these systems cover a great environmental heterogeneity which is essential to sustain their biodiversity. Therefore, we recommend to exhaustively sample the greatest possible variety of environments across different space scales to include even those species restricted to a particular habitat type.

1.3 Diatoms in Tierra del Fuego peat bogs

1.3.1 Prior knowledge

As mentioned previously, the world's largest peatland areas are situated in the Northern Hemisphere (Europe, Asia and North America). Given also the higher concentration of diatom scientists on these continents, there is a high number of studies dealing with diatom of these peat bogs [1.57, 1.71, 1.74, 1.90]. In contrast, studies on diatoms from Southern Hemisphere peat bogs are much scarcer [1.9, 1.49]. In concord with Gaiser & Rühland [1.32], given the high rate of wetlands loss on a global scale, it is essential to double efforts to increase our existing knowledge of their flora. This holds true for high latitude wetlands, where the effect of climate change is so remarkable [1.32], and particularly for good indicators of this phenomenon such as diatoms. The next section will therefore focus on the peat bogs of Tierra del Fuego, South Patagonia.

The province of Tierra del Fuego, Antarctica and the South Atlantic Islands contains 95% of all peat bogs in Argentina [1.82], representing almost 12.5% of the surface of the Isla Grande de Tierra del Fuego [1.45]. Most of these peat bogs are found on the Mitre Peninsula, an area dominated by *Sphagnum magellanicum* peat bogs mostly inaccessible by land. Fuegian wetlands are highly at risk due to increased human activities on a local scale but also following deterioration due to climate change.

Diatom records from Tierra del Fuego (Argentina) are limited, with those concentrated on peatland diatoms even fewer. The oldest study was performed by Cleve [1.16] who studied marine and freshwater diatoms in samples from estuaries around the Río Grande (east coast of Tierra del Fuego), and Isla Desolación (west coast). Most studies were done by Frenguelli who carried out very detailed studies on lakes and streams [1.27, 1.28, 1.29, 1.30] and a core from Río de la Misión, Río Grande peat bog [1.31]. Further historical studies, often restricted to a handful of samples, were performed by Cleve-Euler [1.17] and Krasske [1.54], both reporting on freshwater diatoms present in *Sphagnum* peat bogs. It took then almost five decades to restart diatom research in Tierra del Fuego. Mataloni & Tell [1.70] and Mataloni [1.68] identified and illustrated 113 diatom taxa from different peat bogs. An impressive taxonomic work on South American diatoms was published by Rumrich et al. [1.85] who discussed and illustrated the diatom flora of the Andes from Venezuela to Tierra del Fuego. Although only a limited part of the flora is dedicated to Tierra del Fuego, the book is still considered a standard taxonomic work for those working on its diatom flora. Over the past 20 years, focus was put on specific diatom genera and families in the region such as Achnanthaceae [1.66], Epithemiaceae and Surirellaceae [1.37, 1.39] Orthoseirales [1.40] and the invasive species *Didymosphenia geminate* (Lyngbye) Schmidt [1.36]. In addition to studies dealing with recent diatoms, several studies applied diatoms for paleoenvironmental reconstructions [1.6, 1.23, 1.24].

Our own recent research comprised a study case of diatom communities from Tierra del Fuego-Argentina, the southernmost extensive peatland area in the world. Two dome-shaped peat bogs were studied: Rancho Hambre and Valle de Andorra, which are composed of several shallow ponds in a *Sphagnum magellanicum* matrix to survey their diatom assemblages and their relationship with the environmental parameters at different scales. To this end, diatom communities were compared to those of peripheral limnetic environments (moats; rivers; beaver dams), within peat bog environments (ponds *vs.* moss matrix), as well as within pond habitats (sediments *vs.* periphyton).

In this study, we hypothesized that the ombrotrophic characteristics of the investigated peat bogs impose a robust environmental filtering structuring the present diatom communities, and differentiating them from the surrounding aquatic environments. Furthermore, we postulated that such environmental filters are common to peatlands with similar environmental characteristics within a same region. Thus, we predict that diatom assemblages will be more similar between peat bogs than with those of surrounding environments with different characteristics.

1.3.2 Study area, sampling and statistical analysis

The Valle de Andorra peat bog (54° 45' S, 68° 20' W) is located 6 km from the city of Ushuaia (Tierra del Fuego, Argentina) and is part of the Ramsar-protected site "Vinciguerra Glacier and Associated Peatlands" [1.83]. On the other hand, the Rancho Hambre peat bog (54°47'S, 68°19'W) is located 50 km east from Valle de Andorra and is included within the Valle Tierra Mayor Natural Reserve [1.87]. Both systems were sampled in February 2014 and November 2016. The central area of each of these *Sphagnum*-dominated peat bogs hosts several shallow (less than 2 m deep) ponds. In each peat bog, nine ponds and four *Sphagnum* matrix sites were sampled along a transect across each valley in order to obtain a representative picture of these systems.

In each pond, three samples were taken: one from the plankton, one from the benthos community inhabiting the upper layer of the bottom sediment and one periphyton sample from submerged mosses, including *Sphagnum magellanicum* Bridel, *S. fimbriatum* Wilson and *Sanionia uncinata* (Hedw.) Loeske. In 2016, three peripheral environments were also sampled to compare them with those within the studied peat bog systems. These peripheral sites include a natural ditch/channel running along the periphery of the peat dome (Moat), the river running along each peat bog (River), and a beaver dam built on its margin (Beaver). A complete physical and chemical characterization of the waters was performed at each site, including measurements of temperature, pH, conductivity, total hardness, and ammonium, phosphate, total nitrogen, total phosphorus, chlorophyll *a* concentration and dissolved organic carbon (DOC) concentrations. The corresponding sampling, conservation and measurement methods are described in Casa [1.9].

Samples for light microscopy observation were prepared following the method described in van der Werff [1.103]. Permanent slides were prepared and analyzed as described in Casa et al. [1.11]. Diatom populations of each sample were photographed and measured for later analysis, identification was performed using the currently available literature.

Differences in species composition between groups of samples were visualized through Venn diagrams. Beta diversity was calculated through the Sørensen dissimilarity index (βsor) [1.65, 1.89]. Lower values indicate higher similarities between the compared communities. Then, we calculated the two components of Beta diversity: turnover (βturn) and nestedness (βnest), as they reflect the two primary mechanisms underlying the overall change in species identities across the landscape: the replacement of species or their loss, respectively [1.7].

The relationship between diatom composition and environmental variables was studied using a distance-based redundancy analysis (dbRDA) with Jaccard distance matrix as the response variable. Significantly explanatory environmental features were identified with a stepwise model selection approach. The contribution of each significant feature in shaping the diatom composition was quantified with a permutational multivariate analysis of variance (PERMANOVA) [1.1].

1.3.3 Breakdown of changes in diatom composition between spatial scales

A total of 171 diatom taxa belonging to 52 genera were identified in all the samples (including peat bogs and peripheral samples). Almost 60% of these taxa were present in both localities (Rancho Hambre and Valle de Andorra) (Figure 1.1.A). The most remarkable differences were due to the species turnover between localities (βsor=0.25; %βturn=68; %βnest=32). Sørensen dissimilarity indices and their partitions showed that the diatom flora of each peat bog also differed from that of the peripheral environments (Figure 1.1.B), mainly due to changes in community composition across the different environments, particularly in Rancho Hambre (βsor_{AN}=0.6; $\%\beta turn_{AN}$=65; $\%\beta nest_{AN}$=35; βsor_{RH}=0.54; $\%\beta turn_{RH}$=81; $\%\beta nest_{RH}$=19). Accordingly, the samples from peripheral environments of both localities grouped together on the upper left quadrant of the dbRDA ordination plot (Figure 1.2), indicating that they hosted communities with species compositions compositions clearly different from those of the peat bogs. Consistently, PERMANOVA analysis revealed that the variation of diatom composition between all sites was significantly explained by pH (R^2 = 8.7, P = 0.001), total hardness (R^2 = 3.4, P = 0.016), total phosphorus (R^2 = 3.3, P = 0.015) and conductivity (R^2 = 2.9, P = 0.029).

The highest taxonomic richness in the entire study was observed in Valle de Andorra's beaver dam (AN BEAVER), with 108 species, followed by the connecting Arroyo Grande River (68 species). Both localities are responsible for the higher total species richness of the Valle de Andorra locality compared to that of Rancho Hambre (Figure 1.1.A). Beaver dams are known to affect the hydrological dynamics of rivers, changing the environment from a lotic to a more lentic environment. That way, large amounts of particles can be retained and different diatom floras can develop [1.33, 1.72]. Additionally, unlike the beaver dam in RH, the AN BEAVER was actively occupied by beavers during the study period, increasing its surface between 2014 and 2016. It is therefore possible to hypothesize that, apart from acting as a diatom trap concentrating species from the Arroyo Grande River, AN BEAVER also might get additional species from other sites transported by beavers from different areas inside their home range.

1.3.4 Diatom communities inside the peat bogs

A total of 104 taxa belonging to 36 genera were observed in the peat bog samples. *Eunotia* was the most species-rich genus with 23 species, followed by *Pinnularia* (12), *Nitzschia* (6), *Frustulia* (5), *Gomphonema* (5) and *Neidium* (4). Other genera such as *Fragilaria*, *Brachysira*, *Kobayasiella* and *Encyonema* only had very low species numbers. The observed diatom flora shows, at least based on genus level, a high similarity with that recorded in other peatlands from different regions of the world [1.15, 1.55, 1.57, 1.58]. These communities are usually associated with acid, dystrophic environments with low concentration of nutrients and often related to mosses [1.21, 1.49, 1.93, 1.96, 1.104]. In this study, the diatom composition of the communities observed both in ponds and in the *Sphagnum* matrix was significantly related to low pH, conductivity and total hardness values (Figure 1.2).

A large proportion of the observed diatom taxa could not be identified using the available literature at that time. Detailed analysis using both light and scanning electron microscopy, resulted in the description of several new species in the genera *Aulacoseira* [1.12], *Stauroneis* [1.10], *Frustulia* [1.11]and *Districonella* [1.13]. Analysis of the species in the two largest genera, *Eunotia* and *Pinnularia* [1.9] revealed an additional high number of unknown species that are presently under description (Casa et al., unpubl. res.). Some of these *Eunotia* species were described from the nearby Islas Malvinas/Falkland Islands [1.48] and were also found in the peat bog samples of Tierra del Fuego. Similarly, a high proportion of new species have been observed in Antarctic and sub-Antarctic regions, also known for their very high endemicity and high species richness [1.48, 1.51, 1.97, 1.99, 1.105].

The most commonly reported diatom taxa in the samples include three unknown species of *Eunotia*, *Eunotia tenuivalva* Simonsen, *Chamaepinnularia* aff. *Begeri* (Krasske) Lange-Bert, *Frustulia australocrassinervia* Casa, Mataloni & Van de Vijver , *Tabellaria flocculosa, Kobayasiella micropunctata* (Germain) Lange-Bertalot, the *Pinnularia borealis* complex, *Pinnularia viridiformis* Krammer, *Frustulia delicatula* Casa, Mataloni & Van de Vijver, an unknown species of *Pinnularia* and *Encyonema neogracile* Krammer.

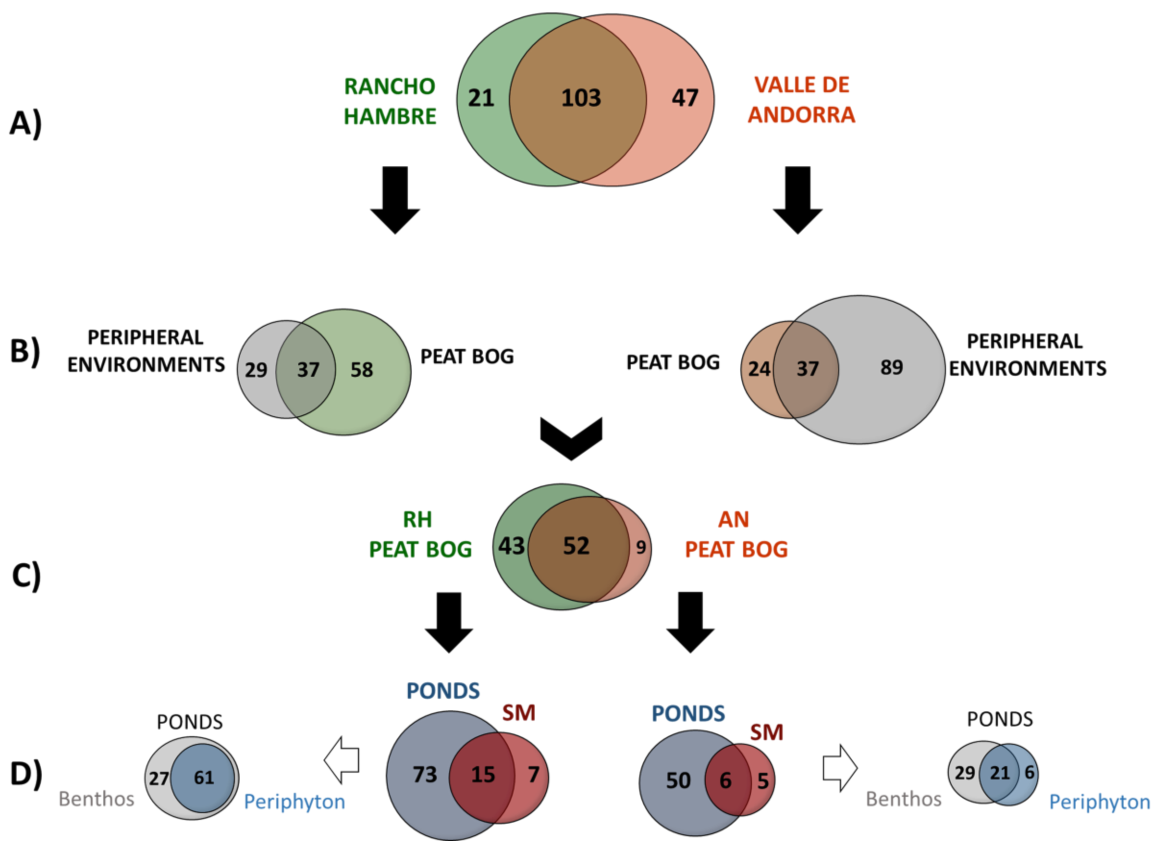

Figure 1.1: Venn diagrams representing a general comparison of the diatom flora between the two localities (A), breakdown of local species composition among each peat bog and its peripheral environments (B), comparison of diatom flora between peat bogs (C) and the comparison between the two landscape components of each peat bog, and among the benthic and periphytic communities of the ponds (D). RH=Rancho Hambre; AN= Valle de Andorra; SM=*Sphagnum magellanicum* matrix.

Despite being 50 km apart and located in different mountain valleys, the composition of both peat bogs showed a high similarity (βsor=0.33; %βturn=44; %βnest=56) and the main cause for dissimilarity between them was nesting. The Rancho Hambre peat bog had a richer community than that of Valle de Andorra, which was almost a subset of the former (Figure 1.1.C). This may relate to a higher environmental heterogeneity in Rancho Hambre as we could observe clear differences in size and trophic conditions of the different ponds, linked to the rugged microtopography of its matrix [1.35]. Ponds in the Valle de Andorra peat bog turned out to be smaller and more homogeneous size than in Rancho Hambre, which may not only provide a narrower range of available niches but also a major influence on the landscape dynamics exerted by the smooth dome of the *Sphagnum* matrix. Indeed, samples taken from the *Sphagnum* matrix (SM) had the lowest species richness (RHSM=22; ANSM=11) (Figure 1.1.D), and were dominated by *Eunotia* sp1 (present in every sample), followed by typically aerophilic limo-terrestrial taxa such as *Hantzschia amphioxys* and members of the *Pinnularia borealis* complex. Remarkably, most diatom communities inhabiting the *Sphagnum* matrix were subjected to the most acidic conditions, the highest conductivity values and total phosphorus concentrations (Figure 1.2). This suggests that the *Sphagnum* matrix is a habitat likely exerting a strong environmental filtering, wherein only few diatom species manage to survive.

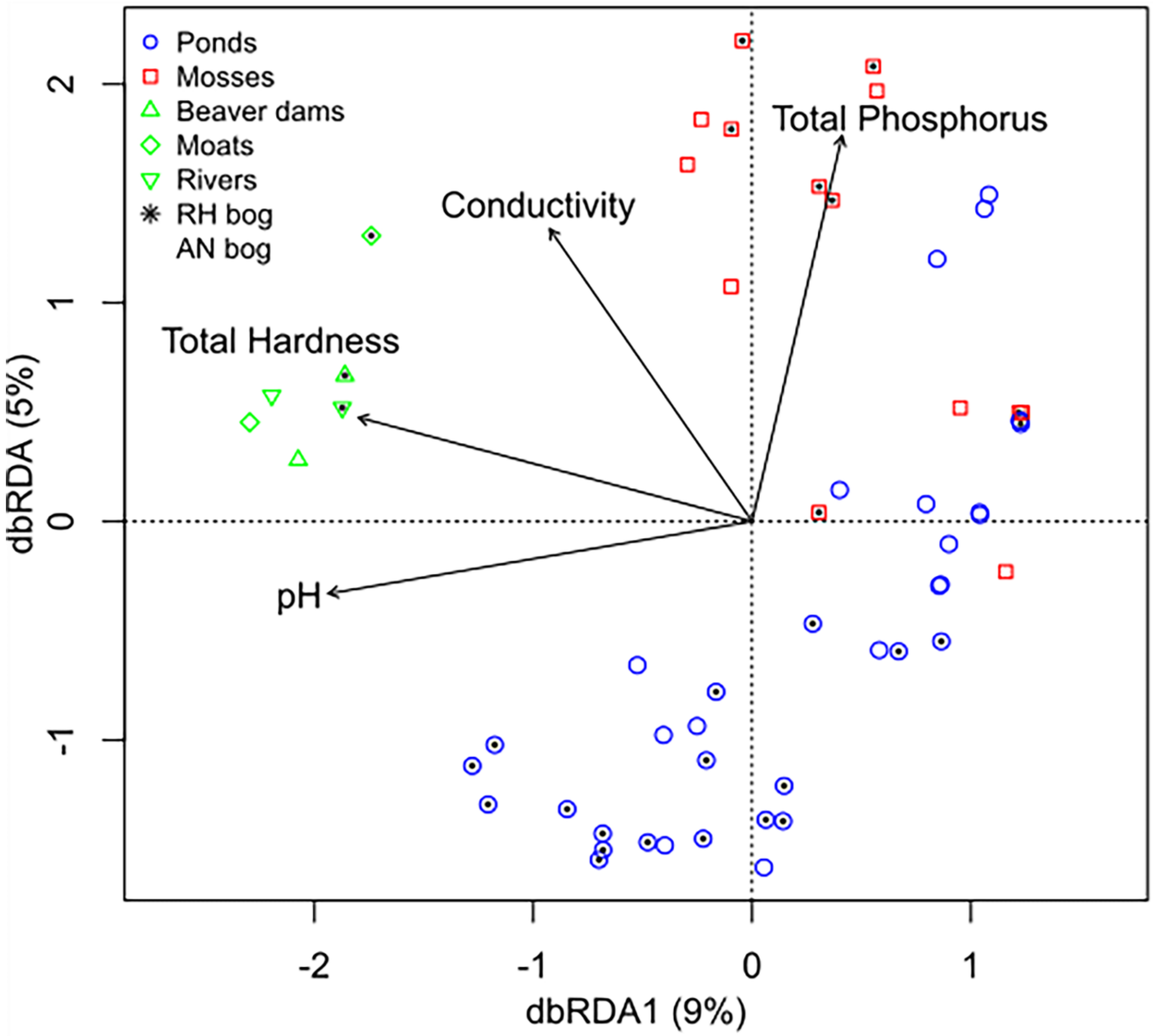

Figure 1.2: Distance-based redundancy analyses (dbRDA) based on Jaccard distance matrix. The environmental features that significantly explained variability in diatom composition were fitted to the ordination. For simplicity, the benthic and periphytic communities were grouped at each pond.

Our results also show that despite their remoteness, there was no limitation on the dispersal of most diatom species between these mountain valleys. Based on this, we postulate that other peat bogs in the region with similar environmental characteristics would present similar diatom communities since the same selection agents would act.

Almost 87.5 % of all observed diatoms could be classified as raphid diatoms. Only one centric species, *Aulacoseira frenguelliana* Casa & Van de Vijver, and twelve araphid taxa were observed in the samples. The latter include *Tabellaria flocculosa*, *Staurosira* cf. *venter* (Ehrenb.) Cleve & Moeller and *Distrionella coxiana* Casa & Van de Vijver. A similar spread over the main diatom groups is commonly observed in other peatlands ([1.25]: [1.56]) owing to the fact that the evolution of the raphe system allowed diatoms to establish themselves in a broader range of substrates, particularly bottom sediments. The colonization by benthic diatoms depends mainly on the availability of a suitable substrate and light penetration [1.4]. In these shallow peat bog ponds, where the incidence of light is not a limiting factor [1.35], the benthic community was by far the richest (88.5% of all peat bog species), and included most of the periphyton species (Figure 1.1.D), thus becoming the most representative community of the studied wetlands.

The plankton diatom community was almost entirely absent as even the genus *Aulacoseira* is mostly regarded as tychoplanktonic. This total absence of diatom plankton was observed in other oligotrophic aquatic environments from the Antarctic and sub-Antarctic regions [1.64, 1.100]. The real ecological reason for this absence is not completely understood but could relate to the low to very low nutrient conditions, the shallowness of the pools or the influence of the wind causing turbulence in the water and preventing the development of plankton [1.95].

Finally, it is unclear whether moss species can have a particular influence on the diatom composition. Some authors have indicated significant relationships between some mosses and diatom species composition [1.78]. In our study, however no such relationships could be found between the different moss species raising the idea that mosses in these peat bogs would only serve as a substrate where the diatom community can be established.

1.4 Closing remarks and future perspectives

Peatlands are biodiversity hotspots; in particular, the acidic, dystrophic, and nutrient-poor environments within peatlands allow the establishment of diverse and unique diatom communities very different from those of nearby aquatic environments. Local environmental conditions are essential in structuring diatom assemblages, with pH and moisture availability as their main drivers. These parameters are closely related to the microtopography and habitat heterogeneity that characterize peatland systems.

Although studies of peatland diatoms have been carried out worldwide, much remains to be learned. This study case showed the extreme importance to consider the diversity of habitats, microhabitats and various communities that make up the peatland system to encompass a greater diversity of species and their ecological preferences.

Improving the knowledge on the autecology and distribution of diatom species is of great importance in a constantly changing world. The more we know about present-day diatoms, the more powerful their use as proxies in paleoenvironmental studies to learn about past changes. Such studies, in turn, contribute to create accurate monitoring tools to protect peatlands from future deterioration.

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