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ORIGINAL PAPER

A new method for monitoring macrophyte communities in small shallow lakes and ponds

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Abstract

Macrophytes are key to the functioning of small shallow lakes (SSLs) because they maintain a clear water state through numerous positive feedbacks. The composition of macrophyte communities changes under anthropogenic pressures; as a result, tools designed to easily and rapidly assess their structure and composition are increasingly requested. We tested three sampling methods (the S_3m sampling method, a stratified method, and a mapped inventory) to monitor macrophytes in 26 SSLs. The effect of each method was evaluated on seven descriptors of macrophyte communities, including the median conservation value. The results were comparable for the three methods, but the stratified method failed to accurately monitor the median conservation value and the number of species present at a low frequency, including exotic and patrimonial species, hence serious consequences for management decisions. S_3m was applied to 262 SSLs ranging from 1 m^2 to 43 ha in surface area. Generalised additive models were used to investigate the environmental factors correlated with four conservation value or ecosystem functioning descriptors. The S_3m method showed that surface area, distance from the source, elevation, and bank verticality were determinants of macrophyte richness. Invasive crayfish impacted the macrophyte richness and the coverage of submerged macrophytes, whereas fish presence increased the macrophyte richness and the percentage of exotic macrophytes and reduced patrimonial interest. S_3m was successfully applied to a wide diversity of SSLs in France. It proved to be rapid, reproducible, and representative for monitoring macrophytes in SSLs. Therefore, it should be applied for SSL management.

Keywords Standing waterbodies · Depressional wetlands · Floristic relevés · Floristic richness · Conservation value

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Introduction

Macrophytes strongly influence environmental characteristics in many ways. They modify substrate and water chemistry—e.g., the dissolved oxygen concentration in the rhizosphere (Rehman et al. 2017)—change biogeochemical cycles (Wetzel and Søndergaard 1998), and contribute to primary and secondary productivity (Peters and Lodge 2010). Macrophytes also provide a substrate for epiphytic algae and their grazers (Wolters et al. 2019), act as a food source for fish and birds (Jeppesen et al. 1998), and offer a physical refuge that buffers interactions between fish and zooplankton (Scheffer 2001). They are involved in various feedback mechanisms that tend to maintain a clear-water state (Scheffer and Carpenter 2003). They also provide numerous ecosystem services (Hilt et al. 2017). Macrophyte composition and abundance recently changed in most waterbodies because of various anthropogenic pressures (Körner 2002) such as eutrophication (Rosset et al. 2014), fish stocking (Williams et al. 2002), or biological invasions (Stiers et al. 2011). Furthermore, fish have a positive influence on floristic richness (Hassall et al. 2011), whereas invasive crayfish have a negative influence on macrophyte communities (Lodge and Lorman 1987).

Macrophyte monitoring programs have been widely implemented in the running waters and lakes of European states following the Water Framework Directive (WFD) (Birk et al. 2012), but they have largely failed to include shallow lakes < 50 ha in surface area (Oertli et al. 2005b) and had little influence on their biological conservation (Hassall et al. 2016). Some methods—e.g., the “Biological Macrophyte Index in Lakes” (IBML) in France (Boutry et al. 2013) and the “Ecological State Macrophyte Index” (ESMI) in Poland (Ciecierska and Kolada 2014)—could be applied for monitoring aquatic plant communities in large shallow lakes so as to evaluate their ecological status. However, they were not designed to evaluate the conservation value of the communities. Small shallow lakes and ponds (SSLs) are major contributors to biodiversity conservation in freshwater ecosystems (Lukács et al. 2013; Panzeca et al. 2021). Moreover, the biological monitoring of aquatic plant communities is still in its infancy in European SSLs despite an urgent need to protect them and to preserve ecosystem services (Hill et al. 2018). This implies monitoring the biodiversity of aquatic plant communities with adapted and efficient methodologies. Apart from Great Britain and Switzerland, most European countries still lack ambitious SSL monitoring tools and programs. The British Predictive System for Multimetrics (PSYM) for ponds (Biggs et al. 2000) and the Swiss “Indice Biologique Etangs et Mares” (IBEM) (Indermuehle et al. 2010) provide contemporary examples of SSL monitoring. PSYM is based on the assessment of the richness of invertebrates and macrophytes and associated trophic ranking scores (Palmer 1992). It can be used to assess ponds with surface areas ranging from 1 m^2 to 5 ha (Biggs et al. 2000). Macrophyte samplings correspond to a simple qualitative inventory (lists of species present in the lake). The IBEM index is valid in Switzerland and its border regions for waterbodies ranging from 300 to 1000 m above sea level (asl). It can be used to assess the floristic richness of SSLs 50 m^2 to 6 ha in surface area and 0.30 m to 9 m mean depth. Neither method can be used to monitor SSLs neglected by the WFD (a few m^2 to 50 ha in surface area). As a consequence, a new method called S_3m (Sampling of Small Shallow lake macrophytes) derived from the PSYM method was proposed and compared with a stratified method derived from the IBEM method (Indermuehle et al. 2010) and with a mapped inventory method (“mapped inventories” hereafter) (Simpson 1991).

Our goal was to test the efficiency of the S_3m method for conducting surveys of plant species composition and abundance in SSLs and calculating diversity and conservation indices. To be applied by a broad range of users, this method should be cost-effective and (1) representative, (2) rapid, (3) reproducible, and (4) flexible. As the choice of the sampling method influences monitoring results and diversity or conservation indices, we compared the S_3m method with two other sampling methods: (1) a sampling strategy inspired by the IBEM method (Indermuehle et al. 2010), (2) mapped inventories with coverages computed with the SIG tool (e.g., Hutorowicz 2020). The comparison was performed across a panel of 26 SSLs. Our first hypothesis was that S_3m would provide a representative picture of macrophyte richness and of the conservation value of plant communities, and be less time consuming than the stratified and the mapped methods. We investigated the key biotic and abiotic factors of the macrophyte communities of 262 SSLs using the S_3m method. Our second hypothesis was that a lower floristic richness and a higher conservation value in high-altitude SSLs would be observed due to harsh climatic conditions. Our third hypothesis was that a high distance from a source—a proxy of SSL connectivity and watershed size—would decrease the conservation value of aquatic plant communities and floristic richness because a high connectivity facilitates biological dispersal and increases nutrient inputs. Our last hypothesis was that the presence of fish and crayfish would reduce the floristic richness and the conservation value of aquatic plant communities.

Materials and methods

Site selection and macrophyte sampling methods

Twenty-six SSLs were selected in southwest France. They represented a large panel of morphometric conditions and considerable variations in water quality (Table 1): surface area from 258 to 95,000 m^2, mean depth from 0.1 to 5 m, shoreline index D (Hutchinson 1975) from 1.04 to 1.88, and various bank slopes ranging from sites with less than 5% of the shoreline with vertical banks (15 sites) to sites with more than 75% of the shoreline with vertical banks (one site). All field data were collected in the summers of 2013–2014.

The S_3m method was applied using a meander method, which is very efficient in detecting rare species (Huebner 2007). Macrophytes were surveyed in a zigzag pattern, regardless of the depth. Deeper water zones were point-sampled. The IBML littoral five-scale from the French norm XPT90-328 classes (AFNOR 2010) was chosen to estimate plant abundance (class 1: a few individuals; 2: isolated small patches; 3: numerous small patches; 4: large discontinuous patches; 5: large continuous patches).

The stratified sampling method used quadrats and transects. The number of quadrats increased with the surface area of the SSL. A grid pattern was fixed with regularly spaced transects, perpendicular or parallel to the longest axis of the SSL. For

Table 1 Summary statistics of the physical features of the 26 selected SSLs. SD = Standard Deviation

	Mean ± SD	Median	Max	Min
Surface area (m^2)	16,579 ± 27,508	4220	95,000	258
Mean depth (m)	1.2 ± 1.1	1	5	0.1
Shoreline index	1.28 ± 0.23	1.21	1.88	1.04
% Banks with slope > 50%	[0–5%] = 15 sites; [5–25%] = 4 sites; [25–50%] = 3 sites; [50–75%] = 2 sites; [> 75%] = 1 site			

each transect, two quadrats were located at each end of the transect, directly against the shoreline, at the usual SSL limit. The SSL shore is usually richer in plant species than the profundal zone (Oertli et al. 2005a), and a higher sampling pressure in this zone determines the stratified strategy. Other quadrats were positioned at each transect intersection. A formula adapted from the IBEM method was used to evaluate the number of quadrats:

$$N_{transect} = 0.3652 \times area^{0.3873}$$

Square-metre quadrats, best fitted for sampling macrophyte communities in lakes, were selected (Ling and Jacobs 2010). In the field, transects were identified with pegs. Only the macrophyte species observed in the quadrats were recorded.

For the mapped inventory, coverages of patches and isolated plants were estimated visually as accurately as possible and drawn directly using a recent aerial photograph of each SSL as a guide (Simpson 1991). Drawings were converted into SIG shape files using QGIS software (QGIS Development Team 2021).

All surveys were conducted by walking on the littoral and shallow zones. Vegetation in the deeper zones was surveyed with a grapnel or a rake from a small boat with an electric motor when the depth was beyond 1.5 m or by free diving. Species such as Characeae, *Ranunculus* subg. *Batrachium*, and mosses were kept in alcohol or dried for identification in the laboratory. All macrophytes (spermatophytes, bryophytes, ferns, and Characeae) were identified to the species level, when possible.

Comparison of the sampling designs

All data were converted into percent coverages. The relative coverage of each taxon from the mapped inventory, expressed as a percentage of the total area, was considered further as the reference data (the most complete and representative one). It was computed with R software (R Core Team 2020) and the sf R package (Pebesma 2018). For the stratified method, the percentage of quadrats occupied by each species was treated as relative coverage. For the S_3m method, a conversion scale (1 = 0.0001, 2 = 0.001, 3 = 0.02, 4 = 0.2, 5 = 0.6) was used. To obtain this scale, each S_3m value was converted into corresponding median values obtained with the mapped inventory from 9 randomly chosen SSLs out of the 26 SSLs. The values obtained with the other 17 SSLs were used for data validation tests. Then, 7 descriptors were selected to identify the effects of the sampling method on macrophyte communities: (1) total floristic richness—a synthetic but quantitative picture of biodiversity –, (2) the Shannon diversity index, (3) the median conservation value according to the national red list, (4) the M-NIP trophic index (Sager and Lachavanne 2009), (5) the percent coverage of submerged species (spermatophytes + Characeae + bryophytes + ferns), (6) the percentage of exotic species, and (7) the richness in 'infrequent species' (difficult to observe because their coverage is $< 1\%$ in mapped inventories). The median conservation value was calculated using the species rarity index (SRI) as follows: (1) all species were assigned a score according to their status on the French national red list, with 32 = CR (Critically Endangered), 16 = EN (Endangered), 8 = VU (Vulnerable), 4 = NT (Near Threatened), 2 = LC (Least Concern), 1 = other, 0 = neophyte; (2) the scores of all species in each sample were summed to provide a species rarity score; and (3) the species rarity score was divided by the number of species recorded in the sample to provide the SRI score (Foster et al. 1989; Rosset et al. 2013).

The sampling methods were compared using Wilcoxon's test and Spearman's correlation between the index values from the mapped inventories and the values from the other two methods, and illustrated with linear regression plots.

Finally, the duration of assessment time is key to the success of a monitoring method. The times needed to implement each of the three methods were compared by measuring the time spent monitoring each SSL (sampling + data entry).

Application of the S_3m method to 262 SSLs: influence of environmental factors on aquatic plant communities

In total, 262 SSLs were selected, differing by their geographical situation and physical features (Fig. 1, Table 2). They were located in various geological bedrocks (acid, calcareous, mixed), under different climatic or altitudinal conditions, and in varied environments (forest, urban, agricultural). They were natural or man-made SSLs, with different hydrological regimes. Twenty-two percent of them dried up in summer. They underwent different biotic pressures (fish, invasive crayfish). Thirteen percent were invaded by exotic crayfish, and 40% harboured fish. Each SSL was sampled once in the summertime. Macrophyte taxa were monitored using S_3m from 2013 to 2020.

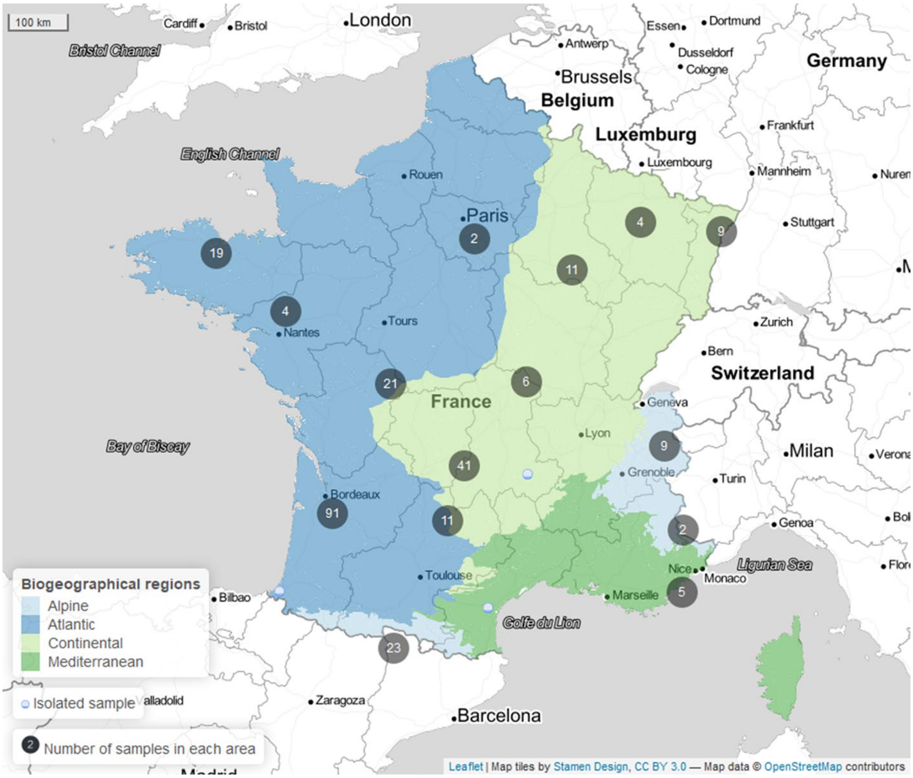

Fig. 1 Localisation of the sampling sites. The number in the circle indicates the number of small shallow lakes sampled in each area

Table 2 Main features of the 262 sites

Environmental factors	Mean ± SD	Median	Max	Min
Surface area (m^2)	17,614 ± 46,172	734	414,100	1
Mean depth (m)	1.0 ± 1.1	0.6	7	0.05
Shoreline index D*	1.34 ± 0.33	1.24	2.96	0.99
% Banks instable or with slope > 50%	0 = 127 sites; 1 = 59 sites; 2 = 34 sites; 3 = 28 sites; 4 = 14 sites			
Elevation (m a.s.l.)	456 ± 670	138	3340	2
Distance from source (km)	33.8 ± 126.2	0.1	950	0
Woodland (%)	44 ± 45	20	100	0
Shade (%)	11 ± 25	0	1	0
Drying	22%			
Invasive crayfish presence	13%			
Fish presence	40%			

*D = Perimeter/(2 * $\sqrt{}$(π * Surface area)

SD standard deviation

The influence of environmental factors (detailed in Table 2) was studied on 4 descriptors: (1) total richness, (2) the SRI score, (3) the percent coverage of submerged species, and (4) the percentage of exotic species.

A generalised additive model (GAM; Hastie and Tibshirani 1999) between floristic richness and 11 environmental factors was used to identify which factors were the best predictors. The best predictors were identified according to the REML method combined with null space penalisation (Marra and Wood 2011). All GAMs were computed using R (R Core Team 2020) and the mgcv package (Wood 2017). Factors were transformed when appropriate, with assessment for normality and homoscedasticity using Shapiro–Wilk tests and histograms. As suggested by Hassall et al. (2011), the GAM was expected to disentangle non-linear relationships between macrophyte richness and biotic or abiotic factors.

The factors were (1) elevation; (2) surface area; (3) distance from the source (DIS) as proposed in Labat et al. (2021); (4) shoreline development index (Hutchinson 1975); (5) shoreline influence estimated with a 5-scale estimation according to the percentage of perimeters with a slope > 50% or instable banks (0 = 0–5%; 1 = 5–25%; 2 = 26–49%; 3 = 50–75%, 4 > 75%); (6) mean depth; (7) 'shade'; (8) percentage of woodland in the SSL surroundings (in a 50-m buffer zone); (9) drying (0 = not known to dry up, 1 = known to dry up); (10) presence of fish; and (11) presence of invasive crayfish (0 = unknown presence of fish or crayfish, 1 = known presence of fish or crayfish). The factors were estimated using at least three field observations during various seasons at the time of macrophyte sampling or according to landowners' observations.

Results

Comparison of the three sampling methods

A total of 148 species—97 helophytes, 33 submerged spermatophytes, 10 bryophytes, and 8 Characeae—were observed in the 26 SSLs used for the sampling comparison. Eight species were exotic, including six infrequent species. According to the French national red list, one species (*Utricularia intermedia*) was vulnerable and three (*Hippuris vulgaris*, *Potamogeton acutifolius*, and *Utricularia minor*) were near threatened. One species (*Caropsis verticillato-inundata*) was restricted to the southwest of France, and it is nationally protected and considered vulnerable on the IUCN red lists. Among these five species, three were infrequent (Table S1). The effects of each sampling method on the macrophyte community relevés are illustrated in Table 3 and Fig. 2.

The coefficient of correlation of each descriptor (richness, Shannon diversity index, SRI, M-NIP, percentage of submerged vegetation, and percentage of exotic species) was higher in the mapped inventory and S_3m results than in the stratified method results (Table 4). The very high correlations ($r = 1$) between S_3m and the mapped inventory based on qualitative data (floristic richness, SRI, M-NIP, percentage of exotic species, richness in species present at low frequencies) confirmed that all species were inventoried by S_3m. Other correlations between S_3m and the mapped inventory remained high, as regards descriptors based on quantitative data such as coverage of submerged species ($r = 0.95$) and the Shannon diversity index ($r = 0.85$). S_3m was well correlated with the stratified method ($r \geq 0.6$, except SRI, $r = 0.45$, and exotic species $r = 0.58$). The correlation between the stratified method and the mapped inventory was weakest for qualitative descriptors such as SRI and the percentage of exotic species ($r = 0.45$ and 0.58, respectively), and was high for M-NIP ($r = 0.84$) and floristic richness ($r = 0.81$). No significant difference between the three methods was obtained for any of the descriptors, except for the Shannon diversity index and the number of species present at a low frequency (Wilcoxon test, $P < 0.005$). The stratified method significantly overestimated the Shannon diversity index compared with the mapped inventory and S_3m (Table 3). The total number of species present at a low frequency was underestimated by the stratified method compared with the mapped inventory and S3m (Table 3). Consequently, three of the eight exotic species and two of the patrimonial species including vulnerable *Utricularia intermedia* were not found by the stratified method. Most of the other exotic or patrimonial species were missed in at least one site (Table S1). The monitoring time was lower with S_3m (mean time = 80 ± 53 min) than with the stratified method (mean time = 180 ± 134 min). The mapped inventory was the most time-consuming method (243 ± 162 min).

Table 3 Mean values and standard deviations of the seven descriptors ($n = 26$ sites) according to the three sampling methods

	S3m	Mapped	Stratified
Total richness	23.85 ± 9.46^{a}	23.85 ± 9.46^{a}	14.61 ± 10.20^{a}
Shannon diversity index	1.86 ± 1.10^{b}	1.38 ± 0.94^{b}	$4.53 \pm 2.06^{***a}$
SRI	2.24 ± 0.35^{a}	2.24 ± 0.35^{a}	2.08 ± 0.25^{a}
% coverage of submerged species	35.41 ± 27.0^{a}	32.67 ± 30^{a}	26.35 ± 22.78^{a}
% of exotic species	3.97 ± 4.95^{a}	3.97 ± 4.95^{a}	4.57 ± 7.30^{a}
M-NIP	2.69 ± 0.15^{a}	2.69 ± 0.15^{a}	2.64 ± 0.18^{a}
Number of infrequent species	19.73 ± 9.22^{a}	19.73 ± 9.22^{a}	$10.34 \pm 5.40^{***b}$

SRI species rarity score; *M-NIP* macrophyte nutrient index for ponds

The corresponding values for rare species (mapped coverage ≤ 1%) are also indicated for discussion. Small letters, significant differences between the descriptors estimated by the stratified method and those calculated by the other two methods (****P*-value < 0.005, Wilcoxon tests)

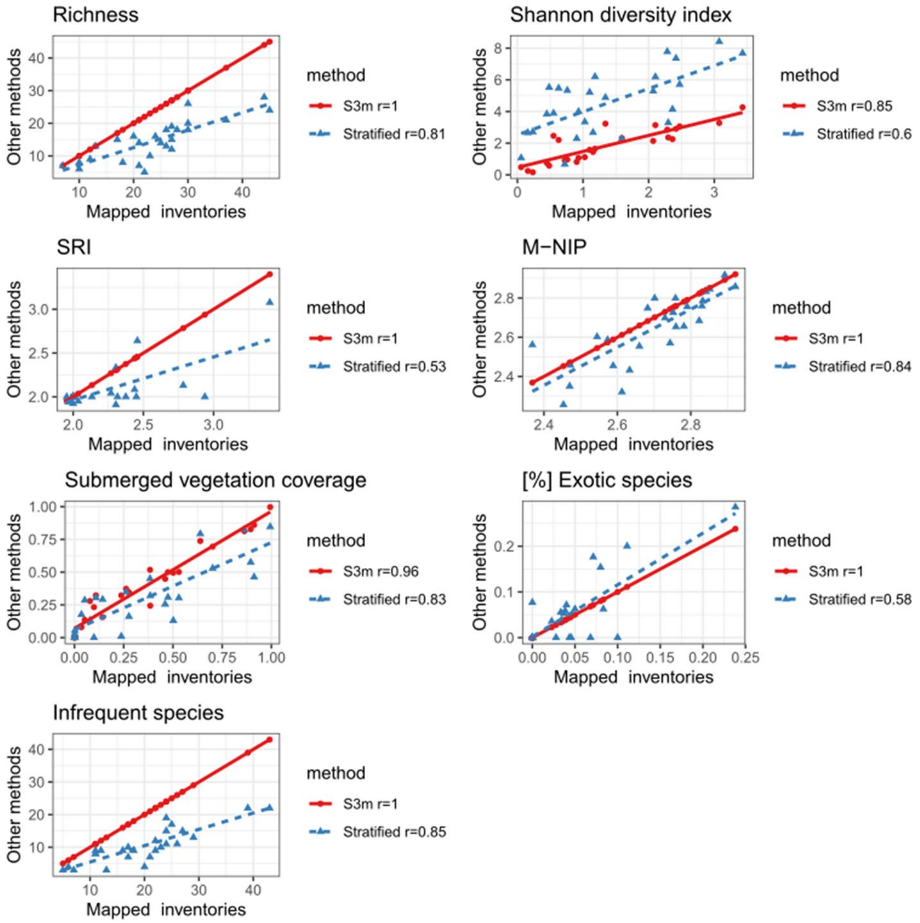

Fig. 2 Linear regression plots obtained for each method compared to mapped inventory results for seven descriptors: total floristic richness, Shannon diversity index, species rarity index according to the French national red list (SRI), trophic index for Swiss ponds (M-NIP), relative coverage of submerged vegetation, percentage of exotic species in relation to total richness, and number of infrequent species. The corresponding Spearman correlation (r) with mapped inventories is mentioned in each plot legend

Influence of environmental factors on macrophyte communities in French SSLs

A list of 238 taxa—40 bryophytes, 20 Characeae, 107 helophytes, and 71 submerged or floating spermatophytes or fern species—was established in all 262 SSLs. According to the national red list, 3 species were considered vulnerable, 9 near threatened, 152 least concerned, 1 data deficient, and 13 exotic.

The mean floristic richness per site was 20 ± 14 taxa, with a minimum of 1 species and a maximum of 73 taxa. Sampling time was usually 30 min to 4 h, with a maximum of 8 h in a very unfavourable context (a 7.4 ha SSL, with most of the shoreline colonised by dense brambles, and the whole waterbody occupied by dense *Ceratophyllum* stands that made it impossible to sail with an electric motor).

Table 4 Correlations between the S_3m, stratified and mapped-inventory sampling methods for the seven descriptors

	Richness			Shannon diversity index			SRI			M-NIP		
	SIG	Strat	S_3m	SIG	Strat	S_3m	SIG	Strat	S_3m	SIG	Strat	S_3m
SIG	1	0.81	**1**									
Strat		1	0.81									
S_3m			1									
SIG				1	0.60	**0.85**						
Strat					1	0.64						
S_3m						1						
SIG							1	0.45	**1**			
Strat								1	0.45			
S_3m									1			
SIG										1	0.84	**1**
Strat											1	0.84
S_3m												1
	Submerged			Exotic			Infrequent Species					
	SIG	Strat	S_3m	SIG	Strat	S_3m	SIG	Strat	S_3m			
SIG	1	0.83	**0.96**									
Strat		1	0.84									
S_3m			1									
SIG				1	0.58	**1**						
Strat					1	0.58						
S_3m						1						
SIG							1	0.85	**1**			
Strat								1	0.85			
S_3m									1			

SIG = mapped inventories. Best correlations are in bold

SRI species rarity score; *M-NIP* macrophyte nutrient index for ponds

GAMs identified 7 key factors of total richness, 6 key factors of SRI, 3 key factors of the coverage of submerged species, and 5 key factors of the percentage of exotic species (Table 5). Fitted relationships are shown in Fig. 3. Surface area was the strongest predictor of total richness, with a logarithmic linear influence. The influence of elevation on floristic richness was not clear from 0 to 1000 m, whereas a clear decrease in floristic richness with increasing elevation was established above 1000 m asl (Fig. 3). DIS—a proxy of SSL connectivity and watershed size—had a positive influence on floristic richness when it was less than 5 km, and a negative effect when it was more than 5 km. The presence of fish favoured floristic richness, whereas the presence of invasive crayfish, a woodland context and bank verticality and instability had negative effects on floristic richness (Fig. 3).

SRI was well explained by environmental factors ($R^2 = 0.23$). Surface area and elevation tended to have a positive influence, whereas the presence of fish, DIS and woodland had a negative one. Mean depth had a positive influence on SRI from 0 to 1.8 m, and a negative one when it was more than 1.8 m. Three factors—invasive crayfish, shade, and

Table 5 Results of the generalised additive model (GAM) describing the four descriptors of macrophyte communities in 262 SSLs in terms of biotic and abiotic factors

	Total richness	SRI	Submerged	Exotic
Surface area	19.28***	0.47*		
Distance from source (DIS)	5.57***	1.03**		3.80***
Elevation	5.08***	2.54***		3.31***
Bank verticality & instability	−3.57***			
Presence of invasive crayfish	−2.57*		−2.36*	−2.28*
Presence of fish	2.11*	−2.34*		3.18**
Woodland	1.50***	0.45*		
Shade			1.88***	
Mean depth		0.84*	0.74*	0.81*
R^2-adjusted	0.71	0.23	0.12	0.38
Explained deviance	0.73	0.25	0.15	0.39

All values are F-statistics, apart from parametric factors (bank verticality & instability, invasive crayfish, and fish presence), which are t-statistics. Significance: $***P<0.001$; $**P<0.01$; $*P<0.05$. Only factors and values with at least $P<0.05$ are indicated

mean depth—had a weak impact ($R^2=0.12$) on submerged species coverage (Fig. 3). A decrease was observed in the submerged vegetation cover along an increasing shade gradient. The impact of mean depth on the submerged vegetation cover was measured when depth was > 1.8 m. At less than 1.8 m depth, the influence of mean depth was positive (Fig. 3). The presence of invasive crayfish reduced the cover of submerged plants.

The percentage of exotic species was favoured by the distance from the source, the presence of fish, and mean depth (Table 5). Elevation and the presence of invasive crayfish tended to limit the percentage of exotic plant species (Fig. 3, Table 5).

Discussion

Comparison of the efficiency of the three sampling methods

SSLs are a matter of concern due to conservation issues, hence the importance of using a sampling method able to detect floristic biodiversity. Moreover, the accuracy and reproducibility of macrophyte coverage estimations are a prerequisite to effectively monitor biological integrity (Karr and Chu 1997). The S_3m method is a rapid assessment method that provides a representative picture of macrophyte richness and structure within the aquatic plant communities of SSLs. These results validate our first hypothesis.

Comparable results were obtained with S_3m and the mapped method to compute species coverage, and they were more accurate and complete than those obtained with the stratified method. Moreover, sampling with the S_3m method required less than half the time required by the other two methods. Species aggregation in patches can strongly affect the accuracy of stratified methods (May et al. 2018). Consequently, the stratified method failed to provide an accurate picture of the conservation value because the sampled richness was incomplete. Moreover, the stratified method failed to consider numerous low-frequency species, so that it underestimated the floristic richness and SRI and overestimated the percentage of exotic species. However, it was accurate for monitoring trophic levels, confirming the relevance of stratified methods for monitoring trophic alterations in various standing water bodies.

Our findings do not allow us to conclude that any one method was best for estimating species coverage. Stratified sampling failed to identify small, isolated vegetation patches and rare species which may represent almost half of the species. However, it was effective in estimating the coverage of dominant species (Pante and Dustan 2012). The mapped and S_3m methods did not include plant density in patches and were poorly fitted to report the coverage of dispersed or low-coverage species. A simple visual estimation can be more representative (Dethier et al. 1993; Bråkenhielm and Qinghong 1995) and less time-consuming (Lillie 2000) than quadrats when the distribution is patchy, at least in small lakes. The accuracy of visual estimation can decrease with increasing surface area (Traxler 1997). The accuracy of the IBML 5-scale can limit this bias. All three methods were valuable for estimating species coverage or at least the coverage of functional groups and dominant species. However, the Shannon index results obtained with the stratified method suggested that stratified methods are less efficient for monitoring community diversity.

A comparison of our S_3m data with literature data showed that S_3m recorded a higher number of plant taxa than other sampling methods did in other studies (Table 6). A comparison of the number of plant species found in literature data with those found using S_3m showed its efficiency for monitoring the macrophyte richness of SSLs. However, these differences are only indicative, and could be explained by different local conditions or geographical isolation (Scheffer et al. 2006; Gledhill et al. 2008).

The accuracy of S_3m is particularly useful to evaluate the conservation value or monitor low-frequency patrimonial taxa or exotic species. However, the inclusion or exclusion of infrequent species in biological monitoring is an old debate (Van Sickle et al. 2007). Deleting infrequent species can alter the sensitivity of community-based methods when it comes to detecting ecological changes (Cao et al. 1998). These species can also play a key role in management decisions when they have a patrimonial value (Thompson 2013).

S_3m is also useful for detecting exotic species early, which is essential for implementing a rapid response and minimising the impact of potential invasive species (Reaser et al. 2020). For instance, two small stands of *Myriophyllum aquaticum* were observed, corresponding to 0.2% of the SSL surface area in one of the 26 SSLs used for comparison. Four years later, its coverage represented approximately half of the surface area. This dramatically increased the cost of its control or eradication and reduced the coverage of other macrophytes such as *Luronium natans*—a species protected at the national scale. Our results from the 26 SSLs highlight that numerous exotic or patrimonial species can be missed when a stratified method is used. Moreover, the exotic or patrimonial species inventoried in the 262 SSLs were mostly infrequent according to their mean coverage (Table S2). Consequently, the use of stratified methods induces serious consequences in management decisions. The S_3m method is cost effective, rapid (less time consuming than the other methods), and efficient for assessing aquatic plant communities in SSLs.

Influence of environmental factors on aquatic plant communities

The higher richness found among the 262 sites vs. the 26 sites (238 vs. 148 taxa) can be explained by the diversity of climatic, elevational, and geological conditions (e.g., Fig. 1).

Our results, from lowly to highly impacted SSLs, confirmed the key role of surface area, elevation, and distance from the source previously established on French lowimpacted SSLs (Labat et al. 2021). The decrease in floristic richness above 1,000 m asl was probably

Fig. 3 Fitted relationships between residuals of the generalised additive models (GAMs) and each significant predictor factor for floristic richness, coverage of submerged species, and species rarity index according to the French national red list (SRI), and percentage of exotic species in relation to the total richness of the 262 SSLs. Solid lines are fitted splines in the continuous factors and fitted values for each of the categorical factors. Dashed lines are standard errors ▶

due to an indirect effect of the short duration of the growing season, cold temperatures (Jones et al. 2003), and maybe lower nutrient availability (Lacoul and Freedman 2005). Despite a lower floristic richness, altitude ponds are often occupied by transition mire and quaking bogs, usually combined with oligotrophic to mesotrophic vegetation in standing waters. This vegetation includes rare or specific species like *Sparganium angustifolium* or *Callitriche palustris* at the highest elevation. Consequently, the conservation value increases with elevation despite lower floristic richness. The influence of anthropogenic pressure cannot be excluded, even if it is usually lower with elevation (Fernández-Aláez et al. 2018). Thus, our second hypothesis was validated.

The distance from the source had an influence on the macrophyte community composition (Labat et al. 2021). Moreover, higher DIS was often characterised by communities typical of natural eutrophic lakes including Magnopotamion or Hydrocharition alliances, whereas lower DIS was characterised by communities of oligotrophic to mesotrophic standing waters including Littorelletea uniflorae and/or the Isoeto-Nanojuncetea. When DIS = 0 (isolated ponds), vegetation was usually typical of natural dystrophic lakes and ponds, or hard oligo-mesotrophic standing waters with benthic vegetation composed of Charophytes. DIS also had a positive influence on floristic richness up to 5 km, and a negative one above 5 km. Our third hypothesis stipulating that distance from the source would influence floristic richness was validated. Connectivity between SSLs and rivers facilitates the dispersal of plant propagules (Vogt et al. 2006), particularly from exotic species (Parendes and Jones 2000). Above 5 km, the effect of DIS on total floristic richness became negative, perhaps because (1) colonisation by invasive species was higher with higher DIS (Fig. 3), and (2) eutrophication was higher because of larger watersheds and increasing anthropogenic pressure. Vertical or unstable banks also impacted floristic richness by reducing the expression of the pool of species (cf. the colonisation gradient based on the littoral depth gradient (e.g., Pokorný and Björk 2010)).

Our hypothesis on the positive effect of fish on floristic richness was validated. This effect had already been found (Linton and Goulder 2000; Hassall et al. 2011). However, the presence of fish could have an impact on the conservation value of the communities, as suggested by our SRI index results. The influence of fish, especially on submerged species, could depend on fish communities. Large cyprinids reduce hydrophyte coverage and composition (Pípalová 2002), whereas their impact on macrophyte communities can be limited by piscivorous fish (Tátrai et al. 2009). Goulder (2001) suggested that higher floristic richness in fishponds can be explained by moderate trampling by anglers. Many anglers or other users can also carry native and exotic plant fragments or seeds on their footwear (Ware et al. 2012) or on their boats. Higher depths motivate boating or sailing for fish or sport, which is a major vector of native and exotic species dispersal (Rothlisberger et al. 2010; Sytsma and Pennington 2015) and can partly explain the positive influence of depth on the percentage of exotic species.

As hypothesised, exotic crayfish had a strong impact on floristic richness, especially on submerged macrophytes and could limit the abundance of exotic macrophyte species. Exotic crayfish can consume and fragment macrophytes, drastically reduce plant biomass and remove some plant species (Carreira et al. 2014). However, no impact of crayfish on

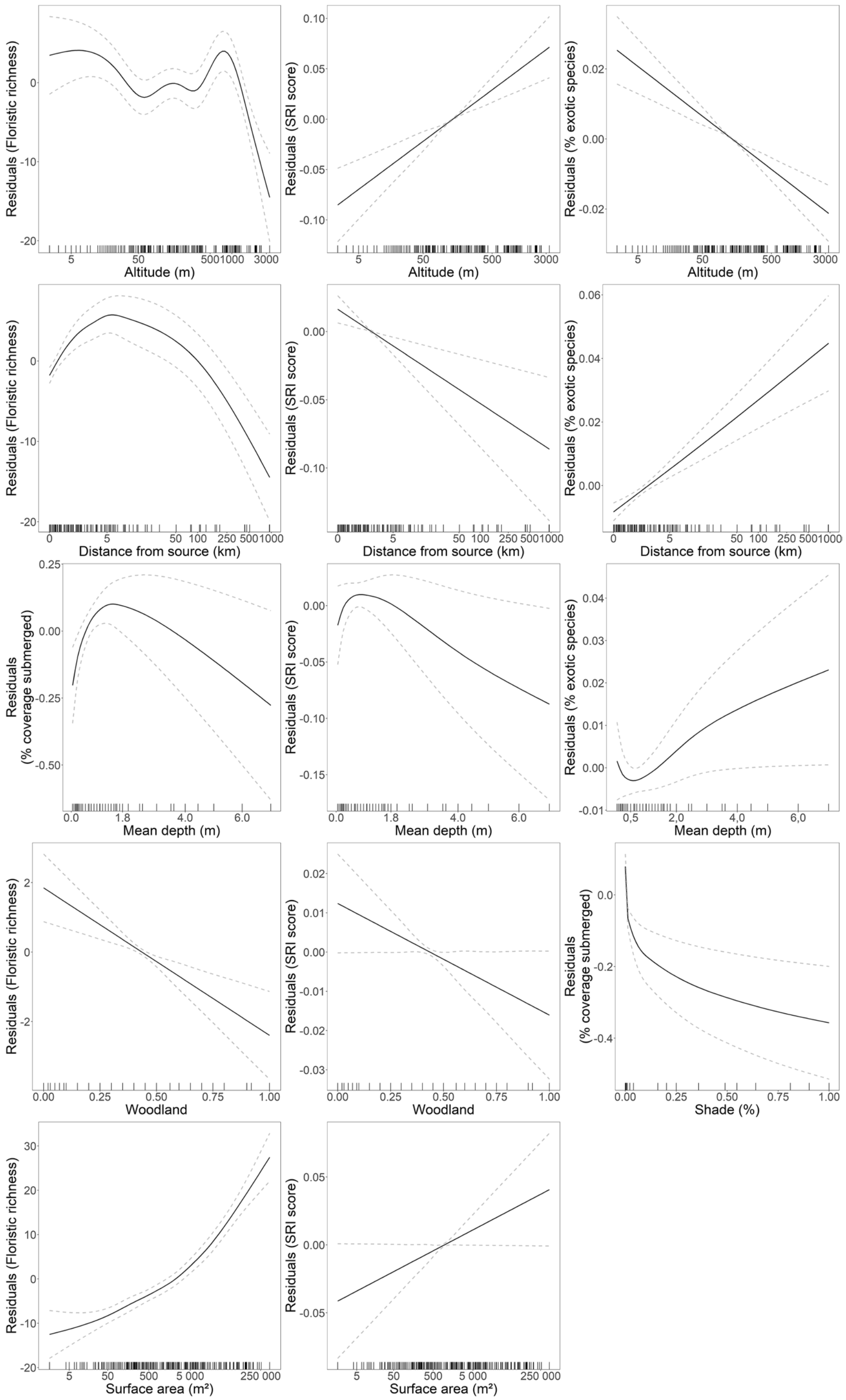
Residuals (Floristic richness)
0
-10
-20
5
50
500
1000
3000
Altitude (m)
Residuals (SRI score)
0.10
0.05
0.00
-0.05
-0.10
Altitude (m)
Residuals (% exotic species)
0.02
0.00
-0.02
Altitude (m)
Residuals (Floristic richness)
Distance from source (km)
0
5
50
100
250
500
1000
Residuals (SRI score)
Distance from source (km)
Residuals (% exotic species)
0.06
0.04
0.02
0.00
Distance from source (km)
Residuals
(% coverage submerged)
0.25
0.00
-0.25
-0.50
0.0
1.8
4.0
6.0
Mean depth (m)
Residuals (SRI score)
-0.15
Mean depth (m)
Residuals (% exotic species)
0.04
0.03
0.02
0.01
0.00
-0.01
0,5
2,0
4,0
6,0
Mean depth (m)
Residuals (Floristic richness)
2
0
-2
0.00
0.25
0.50
0.75
1.00
Woodland
Residuals (SRI score)
0.02
0.01
0.00
-0.01
-0.02
-0.03
Woodland
Residuals
(% coverage submerged)
0.0
-0.2
-0.4
Shade (%)
Residuals (Floristic richness)
30
20
10
0
-10
-20
5
50
500
5 000
250 000
Surface area (m²)
Residuals (SRI score)
0.05
0.00
-0.05
Surface area (m²)

Table 6 Differences in floristic richness observed between studies conducted in France or neighbouring countries

Localisation		Method	Richness	Number of SSLs	Elevation-surface area
Région Centre (France)	Léquivard and Millouet (2013)	Stratified	0 to 31	130	Surface area < 3700 m^2 elevation < 504 m
Neighbouring region	This study	S_3m method	1 to 42	175	Surface area < 3700 m^2 elevation $= 2–3340$ m, $\bar{x} = 441$ m asl
Switzerland	Oertli et al. (2000)	Stratified	2 to 32 (mean $= 11.6$)	80	Surface area $= 6–94{,}346$ m^2 elevation $= 210–2757$ m, $\bar{x} = 732$ m asl
Neighbouring region	This study	S_3m method	1–61 species (mean $= 17.6$)	242	Surface area 6–94,346 m^2 elevation $= 2–3340$ m, $\bar{x} = 441$ m asl

the patrimonial value of SSLs was found by the SRI score, probably because the contribution of submerged species to SRI was generally weak (low richness, and usually a low conservation score). An indirect impact of exotic crayfish on the conservation value is not excluded because submerged species usually shelter numerous invertebrate and fish species (Engel 1988) and strongly influence zooplankton and algal communities (Celewicz-Gołdyn and Kuczyńska-Kippen 2017).

Bank verticality and woodland were also key for plant richness, whereas shade impacted submerged plants. These findings are congruent with literature data (Cowardin et al. 2005; Joye et al. 2006; Angélibert et al. 2010; Hassall et al. 2011; Sender 2016).

The key factors of conservation interest identified from the SRI score should be viewed cautiously. Furthermore, the reliability of red lists in conservation evaluation is a matter of discussion because the red list status is based on expert opinion or political or empirical decision (Le Berre et al. 2019). It might be useful to define rarity as including functional rarity (Loiseau et al. 2020) to better understand the implications of human and natural pressures in SSL functioning or to simply define species sensitivity to alterations, as suggested in numerous integrity indices in North American lakes (Beck et al. 2010) and for depressional wetlands (e.g., Reiss and Brown 2005).

The plants listed in red lists can strongly differ between neighbour countries or regions or according to the scale (regional, national, European). Differences can also be noticed as regards taxa. The French national red list used for SRI computing excludes mosses and Characeae and can miss key factors for these groups or overestimate the influence of factors key to groups included in this red list. Moreover, most of the species in our database were considered LC in the national red list, which tends to have less influence than exotic species in SRI trends. This can be observed through opposite trends for elevation, DIS, mean depth, and fish presence between the SRI and the percentage of exotic species. The SRI score was also influenced by surface area and woodland.

Conclusion

This study proposes and validates a new sampling method (S_3m) adapted to SSLs. S_3m provided similar or even better results than the stratified method and was less time consuming. Therefore, it constitutes an efficient tool for assessing the plant communities of permanent or temporary SSLs. The conservation value of SSLs still remains neglected because of the lack of adapted sampling methods. We tested S_3m on a wide range of French SSLs differing by their locations, physical features, and human uses, and confirmed (1) the importance of biodiversity, including patrimonial species, in SSLs, and (2) that macrophyte richness and submerged macrophyte coverage can be predicted using physical or biological factors.

Large lowland SSLs defined by a short distance from the source, a low coverage of nearby woodlands and the presence of fish harboured potentially higher floristic richness than small mountainous SSLs. Therefore, heterogeneity of the key factors is a prerequisite for the conservation of various communities harboured by SSLs at the landscape level.

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Data availability The datasets generated during and/or analysed during the current study are not publicly available due to private funding but are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest All authors declare that there is no conflict of interest.

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