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Can indicator species predict restoration outcomes early in the monitoring process? a case study with peatlands

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ABSTRACT

Success in ecological restoration is rarely assessed rigorously due to insufficient planning for post-restoration monitoring programs, limited funding and, especially, lack of scientifically validated evaluation criteria and protocols. In this article, we propose the use of the Indicator Value Index technique (IndVal), which statistically determines the association of species to one or several particular site types, to obtain indicators of success at the early stages of the recovery process in restoration projects. Peat bogs extracted by the vacuum method, subsequently restored by a moss-transfer technique and regularly monitored for ~10 years were used as a model system to test this approach. We first identified 34 restored sectors of ~10 ha from 4 to 11 years old in twelve eastern-Canadian bogs. These sectors were then classified according to their degree of success in recovering a typical sphagnum moss carpet (restoration goal). Then, we retrospectively reviewed vegetation communities recorded at the third year after restoration to identify indicator species of different categories of restoration success, using the IndVal methodology. By identifying early indicator species, our method provides a tool that guides intervention soon after restoration if a site is not on a desired successional trajectory. Typical bog species, namely the bryophytes *S. rubellum* and *Mylia anomala* and the tree *Picea mariana*, were indicative of successful restoration; while bare peat, lichens and one species of ericaceous shrubs (*Empetrum nigrum*), which cope better under drier conditions, indicated sites where restoration failed. A surprising finding was that the moss *Polytrichum strictum*, which is known to facilitate the colonization of sphagnum in disturbed peatlands, is an early indicator of unsuccessful restoration. This finding made us question the nursing role of *P. strictum* at a cover threshold above ca. 30%, when *P. strictum* could be outcompeting sphagnum and become dominant. We conclude that the IndVal method is an effective tool to identify early indicators of restoration success when combined with a thoughtful examination of species frequency and cover within each site type.

1. Introduction

Restoration ecology is a young but growing discipline dating to the 1980s (Walker et al., 2007). Despite the increasing number of restoration projects conducted over the last few decades, their success or failure has rarely been evaluated systematically (Bernhardt et al., 2007), due to two main factors. First, recovery of restored ecosystems takes time, and a comprehensive evaluation is not always possible within the project time frame and budget. In fact, most projects are never monitored post-restoration, particularly on a mid- and long-term scale (Palmer et al., 2005; Bernhardt et al., 2005; 2007). Second, restoration goals are usually not clearly defined (Kondolf et al., 2007; Bernhardt et al., 2007). As a result, criteria for judging ecological success are difficult to determine, which jeopardizes the key task of evaluation (Hobbs and Norton, 1996; Hobbs and Harris, 2001) and discourages practitioners from assessing restoration outcomes (Palmer et al., 2005).

Once general agreement on success criteria is reached, indicators to evaluate ecologically successful restoration must be identified (Palmer et al., 2005). Good ecological indicators need to capture the complexities of the ecosystem while remaining simple enough to be easily and routinely monitored (Dale and Beyeler, 2001). Defining these indicators is not an easy task, and some project managers have called for more interaction between practitioners and the scientific community to develop standard monitoring protocols that include efficient indicators of restoration success (Gillilan et al., 2005; Kondolf et al., 2007; Bernhardt et al., 2007). In particular, identifying indicators that could assess the future success or failure of restoration projects at early stages of the recovery process would be extraordinarily useful. Monitoring

Abbreviation: IndVal, Indicator Value Index.

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costs could be reduced and practitioners could be informed soon after implementation of restoration projects of the need to rectify an undesired successional trajectory. Such an iterative process of learning from previous actions is the essence of an adaptive management approach and should be a key element in any restoration planning process (Herrick et al., 2006; Walker et al., 2007; Shafroth et al., 2008; Bernhardt and Palmer, 2011).

A relatively new and simple method to find indicator species was developed by Dufrêne and Legendre (1997): the Indicator Value Index (IndVal). The method combines the species relative abundance with its relative frequency of occurrence to statistically determine species associated to one or several particular site types. The many applications of the IndVal measure in conservation biology were soon recognized by the scientific community (McGeoch and Chown, 1998). However, IndVal measures have only been used occasionally in the evaluation of restoration success (e.g., ants in lignite mine – Ottonetti et al., 2006; spiders in heatlands – Cristofoli et al., 2010; plant short-term indicators in grasslands – Déri et al., 2010; ants in grasslands – Fagan et al., 2010; herbaceous plants in flooded meadows – Metsoja et al., 2012), and to our knowledge, never retrospectively to find early indicators of success in long-term monitoring programs.

Peatlands have been the object of ecological restoration science since the discipline emerged three decades ago (Rochefort et al., 1995). In North America, peatland restoration has, so far, focused mainly on bogs where peat has been extracted by vacuum-milling for horticultural purposes (Rochefort et al., 2003). The objective of bog restoration in North-America has been to re-establish a bog plant community dominated by sphagnum, which would lead to a functional peat accumulating ecosystem through the development of the moss carpet over time (Rochefort, 2000). This led to development of the so called moss layer transfer technique (Rochefort et al., 2003), a restoration approach that has been applied to bogs after peat extraction in both Canada and the USA since the late 1990s. Monitoring has shown that many restoration projects have successfully returned the vegetation community to one dominated by sphagnum (Rochefort and Lode, 2006; Boudreau and Rochefort, 2008; Poulin et al., 2012), but undesired successional trajectories sometimes occur as well (Rochefort, unpublished results).

The goal of this study is to assess the potential of the IndVal methodology to identify early indicators for predicting future restoration success (and failure). Such early indicators should target sites that are not on a trajectory toward the desired plant community and allow practitioners to intervene in the process quickly, to avoid costly losses. Bogs restored by the moss layer transfer technique are good model systems to test IndVal methodology since (1) restoration objectives are clearly defined (return of a dominant sphagnum cover) and (2) restored sites are numerous and have been monitored for more than 10 years.

2. Methods

2.1. Post-restoration monitoring program

We monitored 12 bogs extracted for horticultural peat by vacuum-milling. The milling process breaks up the peat layers of natural peatlands with a rotovator; the numerous pieces of organic soil are then left to dry in the sun and wind. Once dry, the loose peat substrate is collected by large vacuums drawn by tractors. Once commercial peat extraction activities have ceased, sites can be restored using a moss layer transfer technique developed by the Canadian peat industry in collaboration with the Peatland Ecology Research Group (PERG, 2012). Restoration sites monitored were all located in the eastern Canadian provinces of New Brunswick and Quebec (Fig. 1), which are among the highest horticultural peat-producing regions in the world. Most of the studied peatlands developed in lowlands over deltaic sand or silt and clay marine deposits. Classified as Atlantic boreal peatlands and Maritime Atlantic boreal peatlands, they are primarily rainfed, ombrotrophic bogs (National Wetlands Working Group, 1988).

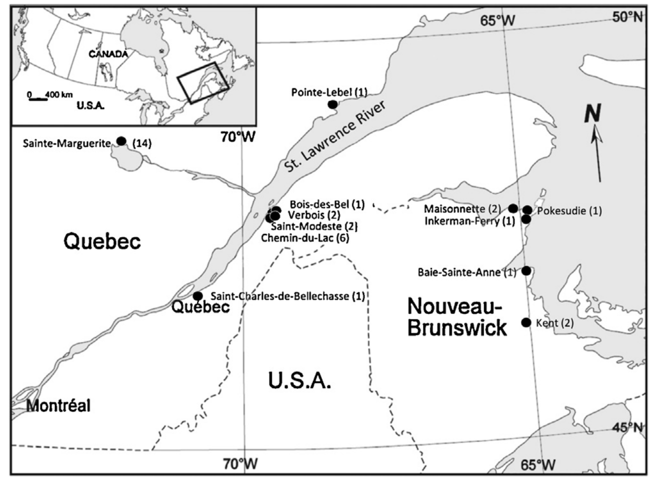

Fig. 1. Location of the 12 bogs previously extracted for horticultural peat and restored by the moss transfer technique in the eastern Canadian provinces of New Brunswick and Québec. Number of monitored sectors per bog in parentheses.

For peat extraction, the bogs were divided into sectors of a few hectares delimited by large drainage ditches (Fig. 2). Sectors formed a relatively uniform hydrological unit. Sectors were abandoned when extraction activities ceased because weakly minerotrophic peat was reached. A restored sector corresponds to this whole unit, restored within a given year, and thus associated with the climatic conditions prevailing during the restoration work. Being spatially and temporally homogeneous, abandoned sectors constitute the unit of restoration work. Restoration using the moss layer transfer technique comprises the following steps: (1) re-shaping field topography and blocking drainage ditches to allow rewetting, (2) spreading plant diaspores including sphagnum previously collected from a donor site, (3) spreading straw mulch to protect diaspores by improving micro-climatic conditions and to prevent desiccation of plant fragment and (4) phosphorus fertilization to favor colonization by plants that nurse sphagnum mosses in some cases (Rochefort et al., 2003). A post-restoration monitoring program documented the evolution of the vegetation community after restoration. Permanent plots of 5 m × 5 m were established, whose number differed among sectors as a function of the sector size and the topographic heterogeneity created during the first phase


Fig. 2. Peat vacuum-extracted site with a drainage ditch surrounding the sector in the foreground.

of restoration work. Vegetation was first surveyed at each permanent plot during the autumn of the third growing season following restoration; and, normally, biannually thereafter. The third year was chosen as the starting point of the monitoring program, since it can be difficult to identify some species, especially developing mosses at earlier stages and with a straw cover still present, and to ensure that well established plants and not ungrounded fragments were recorded. Non-vascular and vascular plants (trees, ericaceous and other shrubs, and herbs) were identified to the species level. Ground cover of vascular plants by vertical projection, as well as peat cover, was visually estimated within four 1 m × 1 m quadrats systematically located within each permanent plot. Cover of all bryophyte including sphagnum and lichen species was recorded in 20 quadrats of 25 cm × 25 cm that were also distributed systematically within the same permanent plots. All recorded species ($n = 64$) or taxa identified to the genus level ($n = 15$), or other level ($n = 3$), are shown in the Appendix A.

2.2. Selection of study sites

Since the late 1990s, PERG has supervised the restoration of close to 60 peatland sectors in 14 bogs across Canada. Only 34 sectors in 12 bogs were included in this study, those that had been restored at least four years prior to their last vegetation survey (Fig. 1, Table 1). Hence, they met the condition of having been surveyed at least twice, allowing us to make retrospective analyses of the vegetation composition and cover. A restored peatland sector has uniform sets of climatic, abiotic, biotic and management conditions associated with it, and follows an individual pattern of plant succession. For this reason, each sector is treated as an independent observation even though most are within the same bog site. In total, our study included 188 permanent plots, and the longest period of time elapsed since restoration was 11 years (Table 1).

2.3. Data processing and statistical analyses

Vascular and non-vascular species and bare peat cover values obtained in the quadrats were averaged for each permanent plot to obtain a database with one row per plot and year of survey and one column per species. For each permanent plot, data collected the third year after restoration and data from the last year surveyed were selected to build two vegetation matrices: *Post 3 yr.* and *Post 4–11 yr.* of dimensions 188 × 72 and 188 × 78 (row × species), respectively.

Our analytical approach included two steps: (1) we classified each plot into different success categories, and (2) we then searched for early indicator species of these different success categories.

(1) In a first step, a Redundancy Analysis (RDA) was run to remove the effect of sector age (year since restoration) from the *Post 4–11 yr.* matrix. A Hellinger's transformation was applied to species cover in order to account for the occurrence of double zeros (Legendre and Gallagher, 2001). The significance of the RDA was assessed using a permutation test with 9999 randomized runs (Legendre and Legendre, 2012). A Principle Components Analysis (PCA) was then carried out on the residuals of the RDA to identify the major vegetation gradients that better represented the 188 plots in the *Post 4–11 yr.* matrix. The RDA residuals were also used to conduct a *k*-means partitioning of the plots into *k* groups that maximized the Calinski–Harabasz index, the best "stopping rules" criterion to determine the most appropriate number of clusters (Milligan, 1996). The obtained *k* groups were interpreted in terms of their restoration success, based on their correlation with vegetation gradients issued from the PCA, thus defining different success categories. Success was defined as the re-establishment of a sphagnum carpet typical of bogs. Typically, sphagnum cover is around 70% in natural peatlands of the study region (Poulin et al., 2005).

(2) In a second step, early indicator species for each success category were sought in the *Post 3 yr.* matrix by means of indicator value indices (IndVal, Dufrêne and Legendre, 1997). For each species *j* in each success category, IndVal computes the product of two values, A_{kj} and B_{kj}. A_{kj} is a measure of *specificity* based on abundance values, whereas B_{kj} is a measure of *fidelity* computed from presence data. IndVal_{kj} ranges from 0 (species *j* not present in any of the objects of the success category *k*) to 1 (species *j* present only in objects of success category *k* and in all of them). The significance of the indicator value of each species was assessed by a randomization procedure with 9999 permutations (Legendre and Legendre, 2012), but we only considered those species with $\text{IndVal} \geq 0.25$ and $P < 0.01$ to avoid the interpretation of species with a weak indicating capacity.

All analyses were carried out using R (version 2.14.0) software (R Development Core Team, 2011). More precisely, ordinations and *k*-means partitioning were run using the functions rda and cascadeKM of the vegan package (Oksanen et al., 2011); the IndVal indices were computed using the multipatt function of the indicspecies package (De Caceres and Legendre, 2009).

3. Results and discussion

3.1. Classification of restored bogs according to previously established criteria for success

The number of years elapsed since restoration accounted for only 4% of the variability in the Hellinger's transformed *Post 4–11 yr.* vegetation matrix (RDA, permutation test, 9999 runs, $F = 8.5667$, $P < 0.001$). This low prediction capacity of time since restoration shows that successional trajectories in restored bogs are clearly identifiable early in the recovery process and are rather stable at the time scale of one decade, with changes in vegetation composition probably being more related to architecture of the different growth forms than to species turnover. This fact suggests that, in this wetland ecosystem, success can be identified with confidence at early stages of the monitoring program. The species more correlated with older sites were mostly woody species that usually grow more slowly, namely the ericaceous shrubs *Chamaedaphne calyculata*, *Ledum groenlandicum* and *Vaccinium oxycoccos* and *Betula* tree species. *Sphagnum fuscum*, a hummock species, was also correlated with older sites, a finding in line with the apparition of a hummock micro-habitat within 10 years post-restoration (Pouliot et al., 2011).

In our analysis, once the effect of time was removed, the first two axes of the PCA carried out with the residuals of the RDA explained 24% and 20% of the variability (Fig. 3). The main gradient (Principal Component 1, PC1) separated the plots dominated by typical bog species (*Sphagnum rubellum* being especially noteworthy; right of Fig. 3) from those dominated by bare peat, in conjunction with *Betula* trees and lichens (left of Fig. 3). A second gradient separated the plots dominated by the pioneer moss *Polytrichum strictum* from those where it was not predominant (PC2, Fig. 3).

The *k*-means partitioning that maximized the Calinski–Harabasz criterion separated the 188 plots into 3 success categories (ellipses, Fig. 3): a first consisting of 107 plots, defined as Successful restoration, mostly on the positive side of the first gradient where *Sphagnum* species dominated; a second with 52 plots, defined as Failed restoration, on the negative side of the first gradient; and a third with 29 plots located on the positive end of the PC2 and defined as *Polytrichum*-dominated plots. Each category is described in detail in the following three sections.

3.2. Early indicators of success in restored bogs

Not surprisingly, *Sphagnum rubellum* was the best early indicator of Successful restoration (Fig. 4a), this species being intimately

Table 1
List of 34 sectors restored by the moss transfer technique in 12 eastern Canadian bogs.

Sector code	Bog	UTM	Sector size (ha)	Restoration year	Age of the restored sector at the time of the last vegetation survey	Number of permanent plots
Atlantic region						
1	Baie-Sainte-Anne	47°01′05″ N 64°52′46″ W	12	2000	10	6
2	Inkerman Ferry	47°42′12″ N 64°49′02″ W	3	1997	9	28
3	Kent	46°18′32″ N 65°08′11″ W	5	2001	10	4
4	Kent	46°18′42″ N 65°08′36″ W	8	2007	4	4
5	Maisonnette	47°49′43″ N 65°02′02″ W	11	2000	10	26
6	Maisonnette	47°49′37″ N 65°01′50″ W	9	2006	5	6
7	Pokesudie	47°48′47″ N 64°46′20″ W	14	2006	5	5
Lowland of Great Lakes/St. Lawrence region						
8	Bois-des-Bel	47°58′03″ N 69°25′44″ W	12	2000	9	32
9	Chemin-du-Lac	47°45′47″ N 69°31′34″ W	3	1997	11	6
10	Chemin-du-Lac	47°45′42″ N 69°31′36“W	1	1999	10	2
11	Chemin-du-Lac	47°45′39″ N 69°31′35″ W	2	2000	10	4
12	Chemin-du-Lac	47°45′37″ N 69°31′30″ W	3	2001	10	3
13	Chemin-du-Lac	47°45′51″ N 69°31′31″ W	5	2002	7	4
14	Chemin-du-Lac	47°45′41″ N 69°31′09″ W	11	2003	7	4
15	Pointe-Lebel	49°07′03″ N 68°11′25″ W	4	2004	7	8
16	Saint-Charles-de-Bellechasse	46°44′53″N 70°59′46″ W	1	1999	10	3
17	Saint-Modeste	47°50′01″ N 69°27′51″ W	1	1997	9	4
18	Saint-Modeste	47°50′02″ N 69°27′50″ W	1	1997	9	2
19	Verbois	47°50′24″ N 69°26′41″ W	9	2005	5	6
20	Verbois	47°50′16″ N 69°26′22″ W	7	2006	5	4
Inland of Northeastern Forest region						
21	Sainte-Marguerite (Section E)	48°48′29″ N 72°10′57″ W	15	2000	10	1
22	Sainte-Marguerite (Section K)	48°48′23″ N 72°10′48″ W	10	2000	10	2
23	Sainte-Marguerite (Section AA)	48°49′29″ N 72°10′47″ W	10	2001	10	3
24	Sainte-Marguerite (Section E)	48°48′45″ N 72°11′13″ W	10	2001	10	1
25	Sainte-Marguerite (Section G)	48°49′06″ N 72°10′52″ W	10	2001	10	2
26	Sainte-Marguerite (Section K)	48°48′11″ N 72°10′38″ W	17	2001	10	1
27	Sainte-Marguerite (Section L)	48°48′07″ N 72°10′54″ W	18	2001	10	1
28	Sainte-Marguerite (Section AA)	48°49′28″ N 72°10′46″ W	10	2002	10	3
29	Sainte-Marguerite (Section H)	48°48′33″ N 72°10′12″ W	12	2002	7	2
30	Sainte-Marguerite (Section J)	48°48′21″ N 72°10′27″ W	27	2002	7	3
31	Sainte-Marguerite (Section AA)	48°49′24″ N 72°10′37″ W	21	2003	7	2
32	Sainte-Marguerite (Section DD)	48°48′45″ N 72°10′51″ W	30	2003	7	3
33	Sainte-Marguerite (Section F)	48°48′36″ N 72°11′31″ W	15	2003	7	2
34	Sainte-Marguerite (Section AA)	48°49′22″ N 72°10′22″ W	21	2004	7	2
						Total = 188

Regions corresponding to major Canadian climatic regions: Atlantic region: mean annual temperature = 4.5 °C, total annual precipitation = 1059 mm, precipitation as snow = 318 mm. Lowland of Great Lakes/St. Lawrence region: mean annual temperature = 3.2 °C, total annual precipitation = 963 mm, precipitation as snow = 270 mm. Inland of Northeastern Forest region: mean annual temperature = 2.3 °C, total annual precipitation = 887 mm, precipitation as snow = 296 mm (Environment Canada, 2012).

related to restoration success in bogs (Poulin et al., 2012; Fig. 3). Although *S. rubellum* was present in almost all plots, it was already three times more abundant in the Successful (mean cover ± SE = 9 ± 1%) than in the *Polytrichum*-dominated (3 ± 1%) and Failed plots (2.5 ± 1%) at the third growing season after restoration (Fig. 4 and Appendix A). *Mylia anomala* was the second best early indicator of success (Fig. 4a), although it played an important role in determining plots as Failed later on (Fig. 3), due to a dramatic increase in frequency and cover with time in those plots (Fig. 4b). Yet, the close examination of sphagnum cushion for species identification in early surveys of successful plots may have biased the estimation of *M. anomala* positively, as this species is often found in between sphagnum individuals. We do know that *M. anomala* thrives easily on dry peat surfaces (PERG, unpublished data), so it may not be considered to be one of the best indicators of success. The typical bog tree species in North America, *Picea mariana*, was found to be the third best early indicator of success. In Successful plots three years since restoration, it was 12 times more frequent (37%) than in *Polytrichum*-dominated plots (3%) and more than twice as frequent as in Failed plots (15%) (Fig. 4 and Appendix A). *P. mariana* is known to require wet soils for germination (Black and Bliss, 1980), likely prevailing in successfully restored sites.

3.3. Early indicators of failure in restored bogs

The use of the IndVal analytical approach also allowed us to identify early indicators of restoration failure, defined as the lack of a typical sphagnum-dominated community. Bare peat and lichens were two such early indicators (Fig. 4b). This was not a surprising finding, since these elements were among the best components segregating Failed plots from the rest in the *Post 4–11 yr.* matrix (Fig. 3). At a >90% of frequency and >0.5 ± 0.0% cover, lichens could be indicative of a less effective hydrological restoration of the site, the main driver of bog restoration (Rochefort et al., 2003; Rochefort and Lode, 2006). The unsuccessful establishment of diaspores of bog species spread during restoration work was ultimately reflected in a greater peat surface area remaining bare of vegetation. The case of bare peat well illustrates the fact that indicators must be interpreted with cautious examination of both their frequency and cover. Bare peat was found in all plots at high cover at the third year. Differences in IndVal were only due to small discrepancies in cover.

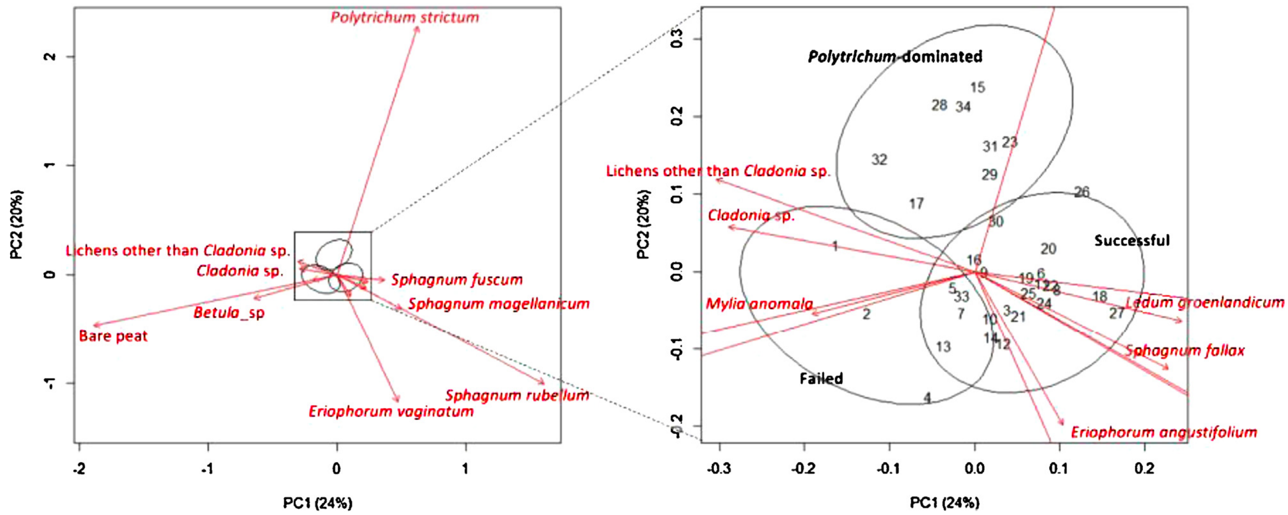

Fig. 3. PC1 vs. PC2 biplot of a partial transformation-based PCA ordination (scaling = 1) of a plant species cover matrix built from 188 observations (permanent plots) in 34 restored peatland sectors by the moss layer transfer technique in eastern Canada. The groups obtained by *k*-means partitioning (success categories) are represented by ellipses that include 95% of the plots belonging to each success category. Peatland sectors were superimposed over the figure at the position of their centroids (site score means). A total of 78 species were identified and hence included in the analyses, but only the 13 species with the highest scores are represented to improve visual clarity.

In fact, bare peat cover was only 12% higher in Failed plots compared to Successful and *Polytrichum*-dominated plots (62 ± 3% vs. 50 ± 3% and 51 ± 4%, Fig. 4, Appendix A). Two species of ericaceous shrubs, namely *Empetrum nigrum* and *Kalmia polifolia*, were also significantly indicative of restoration failure, although they were not among the species that contributed most to the clustering of plots (not represented in Fig. 3). Their significance as early indicators could also be associated to a certain tolerance to the dry conditions presumably prevailing in Failed plots. This might be the case for *E. nigrum*, which typically occurs in the drier areas of bogs where sphagnum do not form a continuous carpet (Bell and Tallis, 1973). However, *K. polifolia* appears more frequently in wet depressions (Marie-Victorin et al., 1995). Due to these facts, and given that differences in frequency of *K. polifolia* between Successful and Failed plots were small (Fig. 4 and Appendix A), we believe that *E. nigrum* is much more reliable as an indicator of Failed restoration than *K. polifolia*.

3.4. Revisiting the role of Polytrichum strictum as a nurse species for Sphagnum re-establishment

In a minority of plots (29 out of 188), restoration could not be clearly classified as a success or failure. In these plots, a single typical bog species was largely predominant: *Polytrichum strictum*, with a mean cover of 60 ± 4% (*Post 4–11 yr.* matrix). As *P. strictum* is recognized as a nursery species for sphagnum establishment (Groeneveld and Rochefort, 2002; Groeneveld et al., 2007), it is difficult to predict the fate of sphagnum, which is found frequently, but scattered throughout these plots. It may be that, above a certain threshold of cover at early stages of the colonization process, *Polytrichum* no longer played a nursing role but was in fact in competition for resources, becoming dominant as the system evolved. In our case, the early cover (i.e., three years after restoration) of *P. strictum* was almost twice as high in *Polytrichum*-dominated plots than in Successful plots (29 ± 3% vs. 15 ± 2%, Fig. 4, Appendix A). In accordance with Groeneveld and Rochefort (2002) who noted the limitations imposed by competition between *P. strictum* and sphagnum, we observed that exceeding a threshold of 29% of cover for *P. strictum* could indicate that restoration by moss transfer technique falls into an alternative stable state (Beisner et al., 2003) dominated by *P. strictum*. Additional intervention could therefore be recommended, such as improving the rewetting of the sector, but corrective measures should be a priori less drastic and more effective than in cases of failure.

Along with *P. strictum*, *Pohlia nutans* was the best early indicator of a *Polytrichum*-dominated trajectory (Fig. 4c), probably in response to fertilization, since both species have been shown to increase in cover along with increased phosphorus input (Sottocornola et al., 2007). *P. nutans* and *P. strictum* could also indicate that hydrological recovery was not successful, as the two species tolerate relatively dry conditions quite well (Tuittila et al., 2000).

4. Conclusions

The IndVal measure is a simple yet powerful tool to search for indicator species that could measure the success of ecological restoration. To identify early indicators of success in restoration projects using this analytical approach, it is essential to establish precise criteria for a clearly defined goal, thereby enabling the classification of sites into success categories. Restored bogs meet this first condition, but this is partly because succession in peatlands usually follows more predictable pathways than is the case in other systems facing stronger disturbances, such as river floodplains. There, the definition of success is more controversial and must integrate a certain level of unpredictability (Hughes et al., 2005). A second condition of our protocol is to have post-restoration monitoring data covering at least two periods, thus allowing retrospective analyses of species composition. By studying the restored ecosystem retrospectively, we obtain indicators that are based on direct observation of successional trajectories and not on inferences from chronosequence studies and space-for-time substitutions, as in previous studies using IndVal to evaluate restoration success (e.g., Ottonetti et al., 2006; Cristofoli et al., 2010; Déri et al., 2010; Fagan et al., 2010). This should increase the strength and reliability of indicators, facilitating adaptive management strategies in restoration projects.

Despite the great adaptability of the IndVal method to different contexts, the identification of indicator species must be complemented with a thoughtful examination of their frequency and cover. Indeed, our analyses have shown that, even after restricting indicator species to those with the strongest indicative

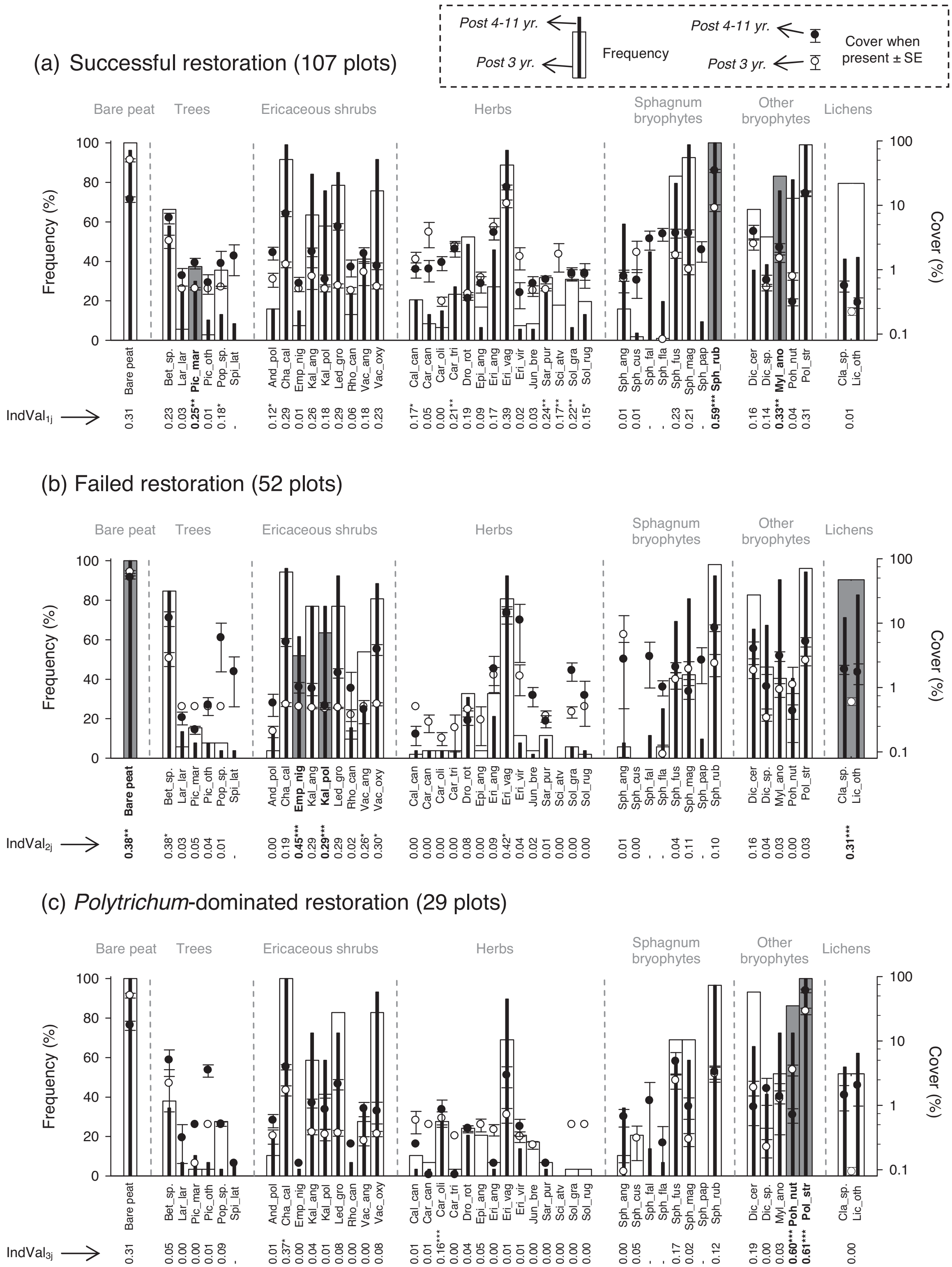

Fig. 4. The most abundant species classified by life form and taxa (plus bare peat) in the 188 permanent plots of 34 restored peatlands clustered in 3 success categories after k-means partitioning: (a) Successful, (b) Failed and (c) *Polytrichum*-dominated plots. Bars represent frequency of occurrence and dots represent cover when present, calculated for the *Post 3 yr.* (open symbols) and *Post 4–11 yr.* matrix (filled symbols). Significant indicator species for each success category are denoted by dark grey wide bars (IndVal method using the *Post 3 yr.* matrix, only species with IndVal > 0.25 and $P < 0.01$ were considered, to avoid including species with a weak indicator capacity, see text; ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$). Note that the cover scale was logarithmic to improve the visual clarity; also, lichens could not be identified to the species or genus level during the *Post 3 yr.* survey and therefore there is only one open bar and one open dot representing the group.

capacity (IndVal > 0.25 and $P < 0.01$), differences in frequency and cover between success categories may be subtle. This may be the result of the division of plots into definite groups (referred to as ‘success categories’ here), which is required in order to compute the IndVal; whereas actual variations in environmental factors between restored sites, and ultimately species distribution, generally follow continuous gradients instead of sharp boundaries.

A second limitation of the IndVal approach paradoxically derives from one of its main advantages: it calculates each IndVal index independently for all species (Legendre and Legendre, 2012), so more than one species may be representative of each success category, as in our case study. How to determine success in cases where indicator species of *different* success categories are found by site managers? Even recent improvements of the IndVal methodology, that suggest using species combinations in addition to single species to find more integrative indicators (De Cáceres et al., 2012), do not solve the problem. How to proceed in a case where species combinations of *different* success categories are found at the restored site? How to determine success in cases where not *all* the species of the significant combination are found at the given site? Our findings warrant future studies to consider the integrity of restored ecosystems while providing practitioners with simple tools to *unequivocally* declare success in restoration projects.

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Appendix A. Supplementary data

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