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Adapting the concept of functionally dominant species for observational data

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ABSTRACT

Conservation ecologists often rely on surrogate species to identify biodiversity hotspots due to the high cost of monitoring programs. While the keystone species approach is an appealing framework for that purpose, it has been criticized for its lack of a clear threshold to identify functionally important species and for its limited ability to handle observational data variability. Here, we propose a modified version of the functionally dominant species (FDS) framework using a bootstrapping random sampling method implemented with either strict or flexible parameters to identify species that disproportionately contribute to the increase or the decrease of biodiversity. We tested our approach on plant, bird, and fish communities of 37 lake-edge wetlands. We identified eight FDS using a 95% confidence interval, of which two displayed a positive contribution to diversity while six had a negative contribution. Using a 99% confidence interval, we found four FDS, all displaying a negative contribution to biodiversity. Most of the identified FDS had ecological or biological traits that support their disproportionate impact on biodiversity. By addressing the limitations of the keystone species framework and providing a statistical framework for analyzing observational data, our method represents a promising tool for conservation ecology.

1. Introduction

Acknowledging that biodiversity monitoring is both resource and time-consuming, the use of surrogate species can prove highly effective in conservation planning (Rodrigues & Brooks 2007). Surrogates consist of single species, or small subsets of species, targeted to assess various ecosystem states such as integrity (Carignan & Villard, 2002; Siddig et al., 2016), functions and services (Feld et al., 2009; Lyons et al., 2005), or biodiversity hotspots (Ceballos & Ehrlich 2006; Myers et al., 2000). Terms such as indicator species, umbrella, flagship, and focal species have also been used to designate surrogate species (Andelman & Fagan, 2000; Lindenmayer & Likens, 2011; Simberloff, 1998). However, identifying candidate species remains challenging due to the lack of consensus on what constitutes a "good" surrogate (Andelman & Fagan, 2000; Cushman et al., 2010; Seddon & Leech, 2008). For instance, while rare and red-listed species have been used as surrogates in conservation planning (Lawler et al., 2003; Lyons et al., 2005; Rodrigues et al., 2006), they are generally poor indicators of an ecosystem's overall state as they often have highly-specialized habitat requirements (Neeson et al., 2018; Orme et al., 2005; Prendergast et al., 1993). Common species have also been proposed as surrogates, with studies suggesting that they better coincide with biodiversity hotspots than rare or top predator species (Tryjanowski and Morelli, 2015) and contribute more substantially to the functioning of ecosystems (Gaston, 2010; Pearman & Weber 2007; Smith & Knapp, 2003).

The keystone species (KS) concept was one of the first attempts to identify surrogate species. The concept was first introduced by Paine (1969) and later redefined by Power and colleagues (Power et al., 1996). A KS contributes disproportionately to ecosystem functioning compared to other species, and the extent of its keystone properties is measured using community importance (CI; Power et al., 1996). This metric quantifies how changes to the relative abundance of a species translate to disproportional changes ($CI > 1$) in a community trait or ecosystem function, such as productivity, nitrogen removal, or species richness.

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While the KS approach has been applied to several communities and ecosystems (e.g., Shukla, 2023), some important challenges remain. For instance, no defined threshold exists to determine what constitutes a disproportionate contribution to ecosystem functioning relative to species abundance (Hurlbert, 1997). Furthermore, the CI metric was developed for data collected from removal experiments, where changes in species abundance and ecosystem functioning are measured before and after the complete removal of a focal species. Such removal experiments can be limiting, as they cannot be generalized to other spatial, temporal, or biotic contexts (Hurlbert, 1997; Power et al., 1996). Evaluating the potential of the CI metric for observational data could broaden its use to existing large datasets of species surveys.

Recently, the KS concept was revisited by Avolio et al. (2019), who proposed to bridge the notion of species abundance and CI. In their framework, the term KS is replaced by the term "dominant species," as they argue that these species influence ecosystem functioning through both a high relative abundance and a large CI. Interestingly, they also suggested that the CI metric may assume negative values (i.e., disproportionate negative effect of a species on an ecosystem function) and be adapted to identify functionally dominant species (FDS) directly from species surveys, rather than from removal experiments. However, they did not provide a clear threshold for species' abundance or CI that would allow these species to be classified as such. Broadening the use of this new framework could improve the identification of surrogate species, guide conservation planning, and help practitioners identify areas where interventions should be prioritized.

In the present study, we proposed a mathematical framework to identify functionally dominant species (FDS). This revised approach can be used to identify surrogate species for ecosystem monitoring and to address the following issues of 1) determining species' abundance and CI thresholds, 2) using observational data rather than removal experiment data, and 3) identifying FDS with a disproportional negative contribution to ecosystem functioning. We tested this approach on the species richness function using observational data collected from three wetland types (alder swamps, ash swamps, and peatlands) and three taxonomic groups (plants, birds, and fishes).

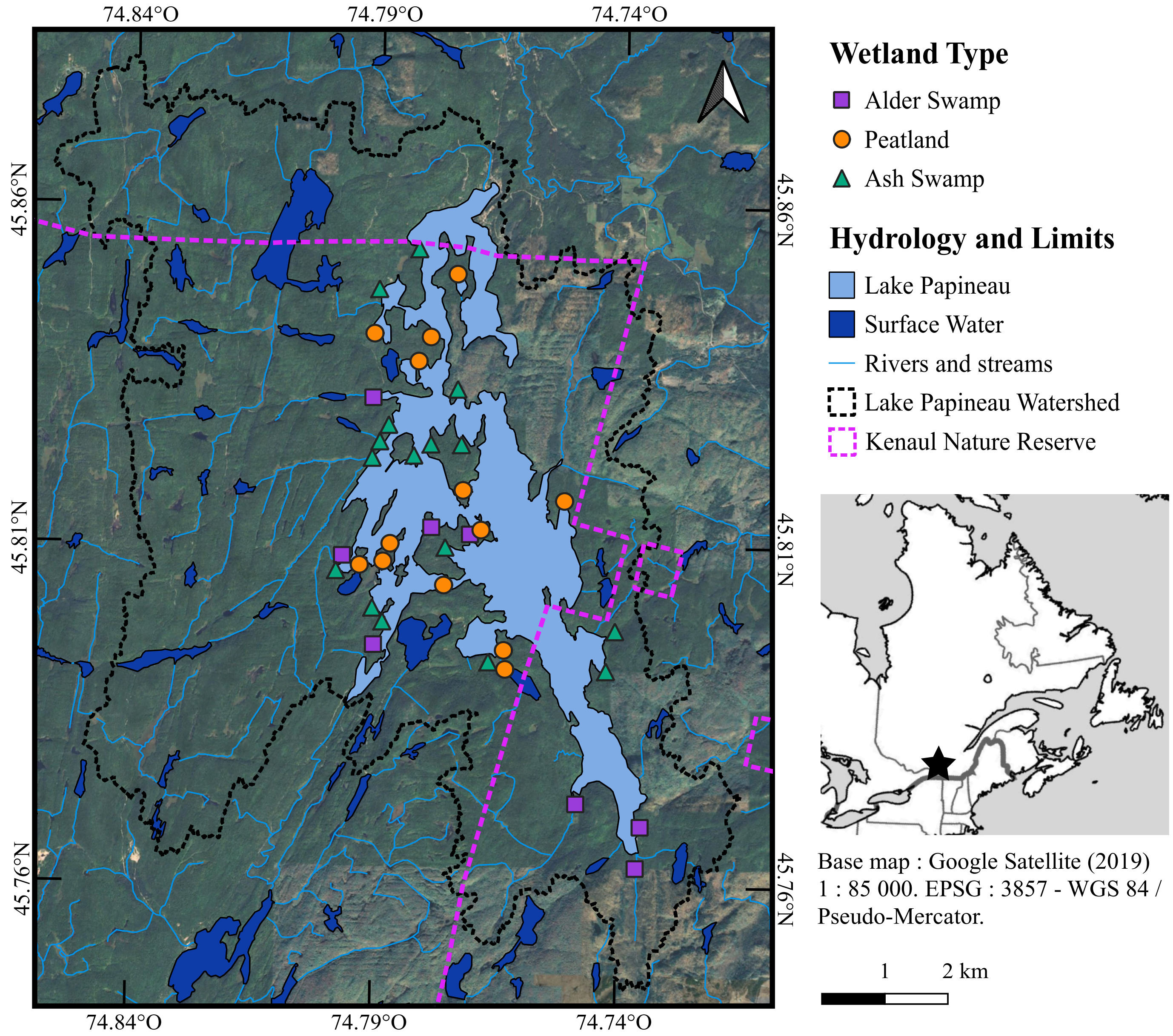

Fig. 1. Location of the 37 lake-edge wetland sites along the shores of Lake Papineau, Québec, Canada.

2. Methods

2.1. Study area

We studied the fauna and flora of wetlands along the shores of Lake Papineau (Fig. 1), a 12.9 km^2 boreal lake (11.2 km length; 3.5 km width; 86.4 km of shoreline; 90 m maximum depth) located in the Canadian Shield of the Laurentian Plateau, in southwestern Québec (Canada). The mean annual temperature of the study area is 4.7 °C, and the average precipitation is 985 mm, of which 18 % falls as snow (Environment Canada, 2021). Lake Papineau's watershed (93.5 km^2) is at the southern limit of the *Acer saccharum-Betula alleghaniensis* bioclimatic region. The lake constitutes 14 % of the watershed area, while the rest is composed of woodlands (72 %), wetlands (10 %), and other small lakes (4 %). The watershed is primarily located within the private fish and game Kenauk Nature Reserve (160 km^2). Housing density around the lake is low (0.5 cottages/km of shoreline), and other human disturbances, such as roads and agriculture, are virtually nonexistent in the watershed. Before 2006, intensive logging activities, such as clear-cutting strips, were conducted in some sectors of the watershed, but these have since been replaced by more sustainable forest management practices.

2.2. Site selection

We targeted our sampling efforts on the lake-edge wetlands of Lake Papineau because their conservation is of particular concern for the stakeholders (Loiselle et al., 2023). We defined lake–edge wetlands as ecosystems where hydromorphic soil and hydrophilic vegetation are present along the edges but are clearly distinct from the lake itself. In the summer of 2018, all lake–edge wetlands were delineated in the field with a global positioning system device using hydrological, pedological, topographical, and botanical characteristics (Dubois et al., 2020). Sites were classified into three types of lake-edge wetlands, which are dominant in the study area. Peatlands (poor fens) typically featured floating mats and were dominated by short ericaceous shrubs and *Sphagnum* mosses. Alder swamps, often connected to streams or influenced by beaver dams, were dominated by dense thickets of *Alnus incana* subsp. *rugosa*. Ash swamps, with low hydrological connectivity to water sources other than Lake Papineau, were dominated by *Fraxinus nigra*, with tree cover reaching at least 30 %. We sampled all peatlands (12) and alder swamps (8), and a subset of ash swamps (16) uniformly distributed around all parts of the lake, yielding a total of 37 wetlands.

2.3. Understory plant communities

We sampled understory plant communities twice during the summer of 2018 (from June 5 to June 22 and from July 20 to August 24). In both surveys, we identified all herbaceous and ligneous species (height < 4 m) in 15 randomly located 0.5 m × 0.5 m plots, for a total of 30 plots per wetland. We only sampled species located in the herbaceous and shrub strata. We compiled the data as presence/absence of each species in each plot (see Dubois et al., 2020 for additional details).

2.4. Bird communities

We sampled bird communities once during the summer of 2019. Half of the sites were sampled simultaneously on June 12 and the other half on the following day. We installed a digital recorder (H2N Handy Recorder; Zoom, Tokyo, Japan) on a tripod 1.5 m above ground for 24 h at each site. We installed recorders about 20 m from the lakeshore and set them to 44.1 kHz sampling frequency. We recorded during optimal meteorological conditions (i.e., clear sky, air temperature > 20 °C, wind < 10 km/h). For each site, we identified species by listening to five audio segments of thirty seconds, randomly selected between 5:00 am and 9:00 am using R 4.0.3 software. We compiled the data as presence/absence of each species in each audio segment. Due to equipment failure, four wetlands were not sampled: three ash swamps and one peatland.

2.5. Fish communities

We sampled fish communities three times during the summer of 2019 (June 26–27, July 10–11, and July 23–24). We adjusted the sampling effort according to the density of hydrological features within the site (i.e., small water channels flowing through the site, small ponds scattered among the vegetation), ranging from one sampling point in sites with one hydrological feature to three in sites with multiple features. We installed a minnow trap at each sampling point during each visit and retrieved it the following day. The individuals caught were identified, counted, and released. We compiled the data as presence/absence of each species in each minnow trap.

The Comité de déontologie de l'expérimentation sur les animaux of the Université de Montréal and by the Ministère des Forêts, de la Faune et des Parcs (MFFP) approved our sampling protocol (SEG permit n°1907SP005GR0).

2.6. Statistical analysis

2.6.1. Relative frequencies and species richness

Functionally dominant species (FDS) must meet both criteria of community importance (CI) and dominance (Avolio et al., 2019). To quantify community dominance, we calculated the relative frequency (RF) from the presence/absence data of each species at each wetland site as follows:

$$RF = \frac{number\ of\ sampling\ units\ where\ the\ species\ is\ present}{total\ number\ of\ sampling\ units\ in\ the\ site} \quad (1)$$

where sampling units represent plots for plants, audio segments for birds, and minnow traps for fish. RF at each wetland site ranged from 0 to 1, with 1 indicating a site where a species is present in all sampling units. We then separated the dataset for each taxonomic group (plants, birds, and fishes) into three subsets based on wetland types (alder swamps, ash swamps, and peatlands). Finally, we calculated species richness as the number of distinct species identified at each wetland for each of the nine data subsets.

2.6.2. Community Importance index

The Community Importance index (CI_i) was introduced by Power et al. (1996) and then adapted by Avolio et al. (2019) as follows:

$$CI_i = \frac{tA - tB}{tA} \times \frac{1}{rA - rB} \quad (2)$$

where *t* refers to the ecosystem function from a site (A or B) and *r* is the RF of the species in these same two sites. Species that contribute proportionally (positively or negatively) to the ecosystem function have CI_i values between -1 and 1. The CI_i of a species is obtained by calculating a central tendency estimator (i.e., average or median) of the values across all pairs of sites. The approach was first developed for removal studies, where A was the control site and B the species removal site, so that $rB = 0$ was always true. The term rB was added by Avolio et al. (2019) to allow the consideration of observational data, where $rB > 0$ is common. However, the term quantifying the ecosystem function ($tA - tB$) was left unchanged, which is problematic in scenarios where a species increases in dominance ($rA < rB$) or where the removal of a species enhances ecosystem functioning ($tA < tB$) (see calculation example in Appendix S1). To address these problems, we propose the following modification to the formula:

$$CI_i = \frac{tA - tB}{tA + tB} \times \frac{1}{rA - rB} \quad (3)$$

One scenario remains problematic in the above equation: when there is no change of relative frequencies between sites ($rA = rB$), leading to a division by zero. To address this issue, we automated the removal of all instances where $rA = rB$ from our calculations, as this procedure has no effect on the calculation of CIi. We then used the above equation to calculate the median CI_i for each species. We did so for the nine data subsets separately (3 taxonomic groups × 3 wetland types). We used the species richness of a sampling unit as the ecosystem function. Therefore, a median CI_i value outside the [-1 to 1] interval indicates that species richness either decreases disproportionally ($CI_i < -1$) or increases disproportionally ($CI_i > 1$) with relative changes in the species' abundances.

2.6.3. Defining CI_i and RF thresholds to functional dominance

While Power et al. (1996) suggested that species should have a CI_i value "much greater than 1" to be considered as keystones, Avolio et al. (2019) proposed that it should only fall outside the −1 to 1 range. Here, we introduced a bootstrap procedure to identify species that contribute disproportionally to the species richness of a community by building confidence intervals around the median CI_i. We generated the distribution by randomly sampling species richness values (with replacement) and re-calculating the median CI_i each time. We repeated this process 9999 times. The final step was to determine whether the true median CI_i value of a species fell outside of the 99 % bootstrap confidence interval. If the median CI_i value of a species is both above 1 and outside of the confidence interval, the species contributes positively to the ecosystem function. On the contrary, if the median CI_i value is both below –1 and outside of the confidence interval, the species contributes negatively to the ecosystem function. To investigate how the confidence interval affects the detection of FDS, we repeated the whole procedure using a 95 % confidence interval.

The method described above allows identifying species that disproportionally contribute to ecosystem functions, either positively or negatively, including those with a low RF. However, following the double threshold approach of Avolio et al. (2019), we considered only dominant species as eligible candidates for functional dominance. Therefore, candidate FDS in each of our nine data subsets needed to 1) disproportionally affect species richness and 2) be among the top five species with the greatest RF.

3. Results

We found a total of 335 plants, 72 birds, and 21 fishes in the 37 lake-edge wetlands sampled around Lake Papineau. Considering a 99 % confidence interval, 12 plant species reported median CI_i values outside of the confidence interval, and therefore disproportionally contributed to plant richness (Table 1). Eight species had a positive contribution ($CI_i > 1$ and above the interval range), and four had a negative contribution ($CI_i < -1$ and bellow the interval range). Among those 12 species, only three found in peatlands (*Chamaedaphne calyculata*, *Carex lasiocarpa* and *Drosera rotundifolia)* exceeded the dominance threshold, i.e., being among the five most abundant species in the community. As such, only the later three species were considered FDS for plant richness, all of which have a disproportional negative contribution on plant richness. In bird communities, only one species (*Vireo olivaceus*), found in ash swamps, reported disproportional negative contribution to bird richness. The species was considered a FDS due to its high RF. No fish met these criteria. Across our nine datasets, the approach therefore identified four FDS based on the 99 % confidence intervals.

When we used the more flexible approach (95 % confidence interval), 49 different plant species contributed disproportionally to plant richness (35 with a positive contribution and 15 with a negative contribution; Table 2). One species (*Onoclea sensibilis*) had a positive contribution in peatlands but a negative contribution in alder swamps. Among these 49 plant species, only four were identified as FDS, and all contributed negatively to plant richness (Fig. 2): *Onoclea sensibilis* in alder swamps; *Chamaedaphne calyculata*, *Carex lasiocarpa,* and *Drosera rotundifolia* in peatlands. Three bird species contributed disproportionally to bird richness and were all found in ash swamps (Fig. 3). Only *Vireo olivaceus* exceeded the RF criteria and was considered a FDS. Finally, five fish species disproportionally contributed to fish richness, and three of them (*Lepomis gibbosus, Umbralimi* and *Perca flavescens*) exceeded the dominance criteria (Fig. 4). We therefore identified a total of eight FDS based on the 95 % confidence interval.

Table 1
Community Importance index (CI_i) of species identified as functionally dominant using a 99 % confidence interval. The sign in the CI_i column indicates whether the species disproportionally affected the species richness of a site positively (+) or negatively (−). Species in bold were among the top five dominant species and met the relative frequency criteria.

	Alder swamps	CI_i	Ash swamps	CI_i	Peatlands	CI_i
Plant	*Juncus effusus*	+10.3	*Fragaria virginiana*	+8.7	*Scutellaria galericulata*	+10.5
			Rumex britanica	−14.2	*Sparganium americanum*	+22.7
					Onoclea sensibilis	+9.1
					Galium palustris	+10.8
					Carex pseudocyperus	+10.6
					Carex brunnescens	+34.2
					Chamaedaphne calyculata	**−2.7**
					Carex lasiocarpa	**−1.9**
					Drosera rotundifolia	**−2.5**
Bird						
	NA	NA	***Vireo olivaceus***	**−2.9**	NA	NA
Fish						
	NA	NA	NA	NA	NA	NA

4. Discussion

4.1. Optimization of the FDS framework

The FDS framework proposed by Avolio and colleagues (2019) suggests that a proportional contribution to ecosystem functioning is sufficient to consider a species as functionally important provided it is among the dominant species of the community. The authors, however, also stated that this threshold is unsuitable for observational data, as it is sensitive to the species' relative abundance. Here, we proposed a modified version of the CI_i to identify surrogate species for diversity monitoring based on observational data. We proposed a bootstrap randomization procedure to construct confidence intervals around the CI_i metric. As expected, our results showed that the quantile of the confidence interval has a strong influence on the determination of FDS, with the total number of candidate species identified increasing from 13 to 57 when using 99 % and 95 % quantiles, respectively. By comparison, increasing the dominance threshold to consider the 15 most abundant species at a given quantile would not affect the results. When combining the two criteria, we identified a total of four FDS at the 99 % confidence interval and eight FDS at the 95 % confidence interval. In general, we believe that the quantile should be chosen to minimize the likelihood of a false discovery rate. Here, we considered the five most abundant species across three wetland types and three taxonomic groups, resulting in a total of 45 species. On this basis, the likelihood of a false discovery rate was of 0.45 and 2.25 species when using 99 % and 95 % quantiles, respectively.

Table 2
Community Importance index (CIi) of species identified as functionally dominant using a 95 % confidence interval. The sign in the CI_i column indicates whether the species disproportionally affected the species richness of a site positively (+) or negatively (−). Species in bold were among the top five dominant species and met the relative frequency criteria.

	Alder swamps	CI_i	Ash swamps	CI_i	Peatlands	CI_i
Plant	*Eupatorium perfoliatum*	+10.3	*Calamagrostis canadensis*	+13.7	*Bidens tripartita*	+13.7
	Glyceria grandis	+16.8	*Erigeron philadelphica*	+1.7	*Carex brunnescens*	+34.2
	Juncus effusus	+10.3	*Fragaria virginiana*	+8.7	*Carex disperma*	+11.1
	Lysimachia terrestris	+2.0	*Galium asprellum*	+3.8	*Carex echinata*	+3.9
	Persicaria sagittaria	+1.9	*Glyceria striata*	+5.0	*Carex intumescens*	+24.7
	Scirpus atrocinctus	+16.8	*Lycopus uniflora*	+3.4	*Carex leptalea*	+5.3
	Agrostis gigantea	−5.5	*Maianthemum canadense*	+6.6	*Carex pseudocyperus*	+10.6
	Eleocaris acicularis	−3.2	*Muhlenbergia Mexicana*	+19.3	*Galium palustris*	+10.8
	Fraxinum nigra	−2.5	*Oxalis stricta*	+4.4	*Galium trifidum*	+3.3
	Onoclea sensibilis	**−1.6**	*Persicaria sagittaria*	+3.2	*Hypericum ellipticum*	+11.5
	Parthenocisus vitacea	−18.6	*Alisma trivialis*	−51.1	*Lycopus uniflora*	+2.6
			Aralia nudicaulis	−9.8	*Onoclea sensibilis*	+9.1
			Carex lupulina	−4.2	*Rubus pubescens*	+3.9
			Carex lacustris	−20.0	*Sagittaria latifolia*	+15.8
			Galium trifidum	−6.1	*Scutellaria galericulata*	+10.5
			Rumex britanica	−14.2	*Sium suave*	+8.3
					Sparganium americanum	+22.7
					Thelypteris palustris	+4.8
					Ulmus americana	+28.2
					Veronica scutellaria	+9.1
					Viola canadensis	+4.4
					Carex lasiocarpa	**−1.9**
					Chamaedaphne calyculata	**−2.7**
					Drosera rotundifolia	**−2.5**
					Lycopus clavatum	−19.1
					Utricularia intermedia	−7.8
Bird	NA	NA	*Corvus corax*	+3.7	NA	NA
			Setophaga petechia	+1.6		
			Vireo olivaceus	**−2.9**		
Fish	*Pimephales promelas*	+3.9	*Ambloplites rupestris*	+5.9	***Umbra limi***	**+1.2**
	Lepomis gibbosus	**−1.5**	***Perca flavescens***	**+1.4**		

4.2. The ecology of FDS

The community importance index (CI_i) implemented here tells the fraction of the local species richness pool that is gained (CI_i positive) or lost (CI_i negative) as the focal species increases in relative abundance. This conceptualization of functional dominance is fundamentally different from the keystone species concept originally proposed by Paine (1969), which relates to trophic interactions. On one hand, species at low relative community abundance may have a large CI_i index only by chance as they are found in a limited number of sites. These extreme CI_i values are purely statistical and do not underline any ecological mechanisms. On the other hand, species at high relative abundance tend to show CI_i values closer to the [-1, 1] interval. While dominant species have been associated with biodiversity hotspots (Gaston, 2010; Pearman & Weber 2007, Smith & Knapp, 2003), they can also negatively affect species richness through different ecological mechanisms (Avolio et al., 2019; Gaston, 2011; Grime, 2002; Hillebrand et al., 2008; Tilman, 1982). For instance, dominant species may contribute negatively to species richness ($CI_i < -1$) through competition for resources and space or through niche modification that is only favorable to them (Avolio et al., 2019; Martin et al., 2023; Ulrich et al., 2010). However, dominant species may also contribute positively to species richness ($CI_i > 1$) through facilitation via the mobilization of resources for other species or through niche specialization in harsh environments (Avolio et al., 2019; Tokeshi, 1990). As such, we believe it is useful to distinguish between species that positively or negatively contribute to biodiversity while also carefully evaluating the potential biological and ecological mechanisms involved. Finally, as no species exists in isolation, the proposed methodology allows the identification of a set of surrogate species that might better consider the interactions associated with species distribution and habitat suitability (Morelli and Tryjanowski, 2015).

4.3. Plant communities

All species identified as functionally dominant in the present study contributed negatively to plant richness. In alder swamps, *Onoclea sensibilis* was the sole FDS identified. It was the second most abundant species (RF = 0.093), behind *Alnus incana* subsp. *rugosa* (RF = 0.102). While native to the study region, *O. sensibilis* is often considered an undesirable weed because it can rapidly dominate the understory vegetation (Holland & Burk, 1990; Lellinger, 1985), especially following disturbances (Burk, 1977; Huppert et al., 2020). This shade intolerant species can spread rapidly through both rhizomes and sexual reproduction (Lellinger, 1985; Khrapko & Tsarenko, 2015) and has been shown to be highly competitive for resources (Cousens et al., 1985). As such, its negative contribution to species richness in alder swamps is likely linked to its competitive acquisition of resources and space (Grime, 2002; Tilman, 1982).

In peatlands, three FDS were identified using both the strict and flexible approaches: *Chamaedaphne calyculata* (RF = 0.108), *Carex lasiocarpa* (RF = 0.083), and *Drosera rotundifolia* (RF = 0.080). All three species are typical of lake-edge peatland vegetation (Crow & Hellquist, 2023; Davis, 2016). *C. calyculata* is a dwarf shrub that forms dense, dome-shaped, clonal thickets (Crow & Hellquist, 2023) that spread through rhizomes (Bell et al., 2011). It is considered a competitive species that can respond quickly to nutrient addition in poor ecosystems (Bartsch, 1994). Its leaves are semideciduous, meaning that individuals tend to retain a portion of their leaves through to the next growing season, which affects the recycling of nutrients. This shrub has also been linked to hummock formation (peat mounts) through the accumulation of *Sphagnum* mosses bellow its branches (Kenkel, 1988), and to the formation of floating mats invading open waters, with adventitious roots buried in *Sphagnum* mosses(Swan & Gill, 1970). Communities dominated by leatherleaf and *Sphagnum* mosses are generally species poor (Pellerin et al., 2009). *C.lasiocarpa* is also involved in early peatland

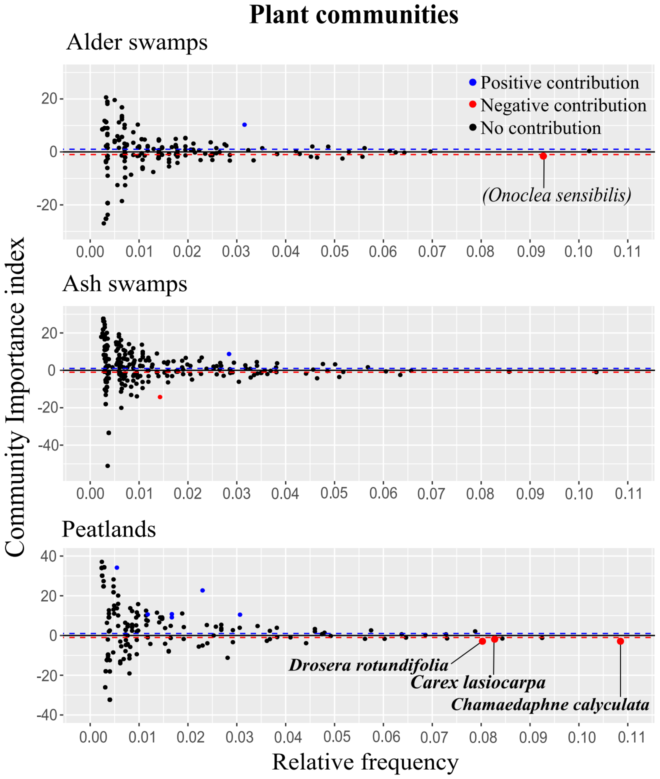

Fig. 2. Community Importance index (CI_i) of plant species by wetland type relative to their maximum relative frequencies (RF). The names of functionally dominant species (FDS) identified using the 95% and the 99% confidence intervals are indicated. FDS that were only identified using a 95% confidence interval, but not with the 99% confidence interval, are shown in parenthesis. Blue points: FDS positively contributes to plant richness; Red points: FDS negatively contributes to plant richness.

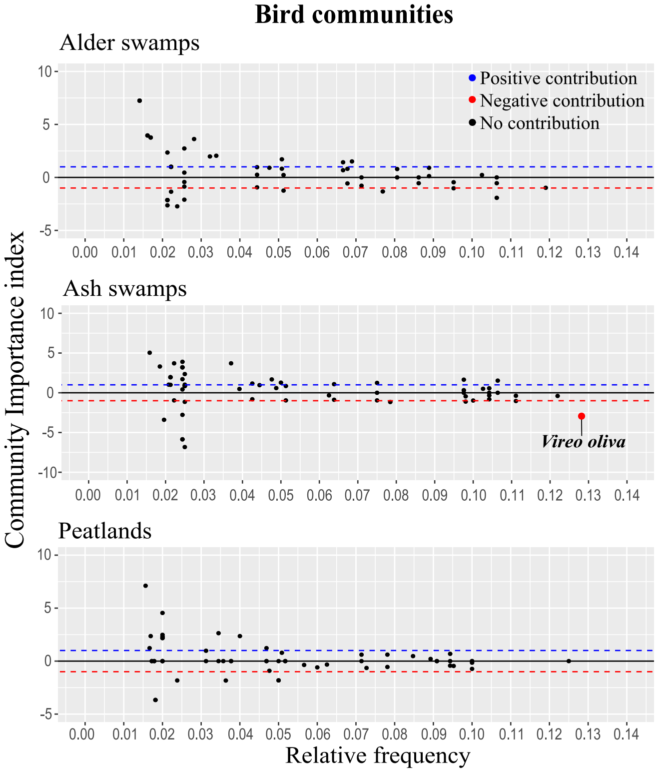

Fig. 3. Community Importance index (CI_i) of bird species by wetland type relative to their maximum relative frequencies (RF). The names of functionally dominant species (FDS) identified using the 95% and the 99% confidence intervals are indicated. FDS that were only identified using a 95% confidence interval, but not with the 99% confidence interval, are shown in parenthesis. Blue points: FDS positively contributes to plant richness; Red points: FDS negatively contributes to plant richness.

development and the formation of floating mats (Bedford et al., 1988; Swan & Gill, 1970; Wang et al., 2015). It is a tall herbaceous species often dominant in bogs, fens, and lake shore vegetation (Bedford et al., 1988). It can spread vegetatively and tends to form dense monospecific colonies that expand laterally through rhizome propagation. In stressful environments, such as during prolonged floods or droughts, *C. lasiocarpa* can be highly competitive, leading to lower species richness and higher community evenness (Luan et al., 2013; Wang et al., 2010). Altogether, the ecological traits of *C. calyculata* and *C. lasiocarpa* support their role as FDS through competition for resources and niche modification via autogenic processes related to peatland development.

The role of *D. rotundifolia* as a FDS is less clear. This small carnivorous species is widely distributed and thrives in ecosystems with low nutrients and acidic soils (Baranyai & Joosten, 2016). It is associated with a high cover of dwarf shrubs and *Sphagnum* mosses (Baranyai & Joosten, 2016; Crowder et al., 1990; Stewart and Nilsen, 1992). As such, *D. rotundifolia* is most likely a companion niche species of *C. calyculata*, with a low impact on community structure.

4.4. Bird communities

In bird communities, both the strict and flexible approaches allowed the identification of one FDS: *Vireo olivaceus*. This species was the most abundant in ash swamps (RF = 0.128) and negatively contributed to bird richness. *V.* is one of the most common species found in forested habitats of northeastern America (Boreal Songbird Initiative, 2023; Cornell Lab of Ornithology, 2023). It is a persistent singer that occupies the soundscape of forests and displays aggressive territorial behavior toward other bird species (Barlow & Power, 1970; Boreal Songbird Initiative 2023). For instance, they may intimidate other species through flight chase, crest-erected alerts, head forward threats, tail-fanning, and gaping (Barlow & Rice, 1977). These competitive behavioral traits could explain why it was abundant in sites with lower bird richness.

4.5. Fish communities

The procedure identified three fishes as FDS using the flexible approach, but none using the stricter approach. In alder swamps, *Lepomis gibbosus* negatively contributed to fish richness. The dominance of this species is likely related to resource appropriation and trophic interaction, as it competes with other fish species for food and habitat, with adults often forming large schools in littoral zones and preying on other fish and eggs (Copp et al., 2004; Jordan et al., 2009). While the species is native to northeastern Canada, is it considered invasive in western parts of the country (Jordan et al., 2009).

Perca flavescens was identified as a FDS in ash swamps, which positively contributed to the richness of fish species. The habitat characteristics of the sampled wetlands could explain this result. While its diet changes with age, size, and habitat (Keast, 1977; Shrader, 2000; Brown et al., 2009), in pelagic, unproductive systems such as Lake Papineau's wetlands, juveniles typically feed on large zooplankton and macroinvertebrates. This behavior can influence the trophic structure of invertebrate communities in these habitats, leading to shifts in the diet of other fish species (Shrader, 2000). However, in areas dominated by aquatic vegetation, such as ash swamps, its foraging efficiency is reduced, and its diet becomes more diversified (Diehl, 1992), allowing other species to compete for resources. Therefore, *P. flavescens* could contribute positively to fish richness in ash swamps through facilitation and mobilization of resources via trophic interactions.

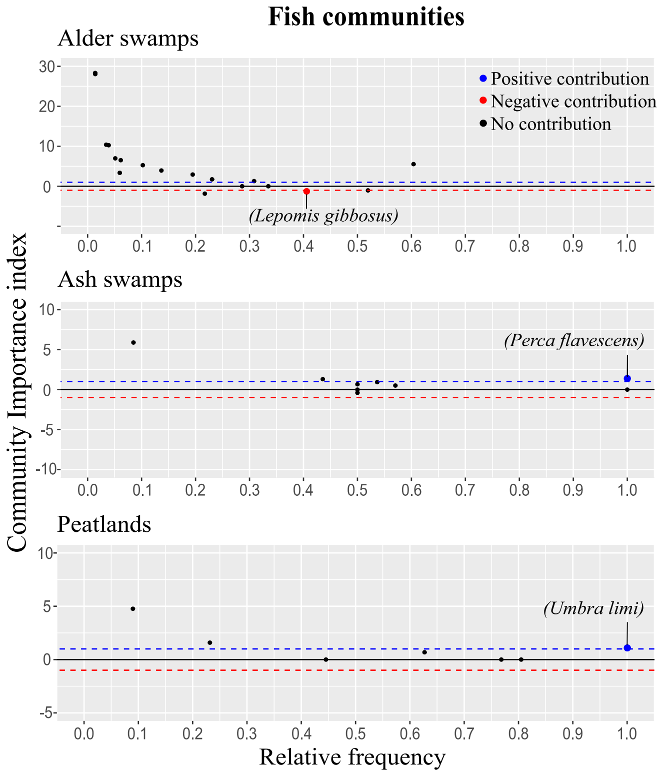

Fig. 4. Community Importance index (CI_i) of fish species by wetland type relative to their maximum relative frequencies (RF). The names of functionally dominant species (FDS) identified using the 95% and the 99% confidence intervals are indicated. FDS that were only identified using a 95% confidence interval, but not with the 99% confidence interval, are shown in parenthesis. Blue points: FDS positively contributes to plant richness; Red points: FDS negatively contributes to plant richness.

Finaly, the procedure identified *Umbra limi* as a FDS in peatlands, which positively contributed to the fish richness of these wetland communities. While this species primarily feeds on invertebrates, it can also feed on other fish species (Becker, 1983) and can be found in various shallow habitats (Peckham & Dineen, 1957). A key feature of this species is its strong preference for harsh ecosystems, such as those with low oxygen and low pH, conditions commonly found in the peatlands we studied (Rahel, 2000; Tonn et al., 1990). This species is capable of breathing air bubbles when oxygen levels are particularly low (Magnuson et al., 1983). Therefore, *U. limi* is likely a niche species that helps to increase fish richness in peatlands, habitats are generally too harsh for most fish species.

5. Conclusion

This paper presented a modified version of the FDS framework that identifies surrogate species for ecosystem monitoring. The procedure could be adapted to identify FDS in other ecosystem types, using different taxa, and for a vast range of ecological functions. Given that species surveys are widely available for many taxa, regions, and ecosystem types, we believe our approach represents a valuable tool for applied ecology. Our findings emphasize the importance of studying the ecology of potential FDS candidates. A closer inspection revealed three strong competitor plant species with a disproportionate negative effect on species richness in alder swamps (*Onoclea sensibilis*) and peatlands (*Chamaedaphne calyculata* and *Carex lasiocarpa*). The red-eye vireo (*Vireo olivaceus*) was also revealed as a strong competitor species in swamp ecosystems. In fish communities of both ash- and alder-swamps, *Perca flavescens* plays a role of facilitating resources transfer and mobilization. Finally, we identified two FDS niche species in peatlands. The first is a carnivorous plant species (*Drosera rotundifolia*) found in species-poor communities of peatlands. The second is a stress tolerant fish species (*Umbra limi*) found in hypoxic waters.

CRediT authorship contribution statement

Audréanne Loiselle: Writing – review & editing, Writing – original draft, Methodology, Investigation, Data curation, Conceptualization. **Raphaël Proulx:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Stéphanie Pellerin:** Writing – review & editing, Resources, Project administration, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2025.113271.

Data availability

Github

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