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Synergies and trade-offs among ecosystems functions and services for three types of lake-edge wetlands

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ABSTRACT

Wetlands are the world's most important providers of ecosystem functions and services (EFS) and the most threatened ecosystems. Systematic conservation planning strategies are urgently needed to identify efficient strategies that optimize EFS provisioning in wetlands. Evaluating synergies and trade-offs among EFS indicators provides an ideal framework, as they highlight the challenges faced by conservationists. However, associations between indicators often vary across region, scale, and ecosystem type. In this study, we compared the provisioning of eight EFS of three types of wetlands to evaluate the influence of indicator choice and aggregation on synergies and trade–offs. We quantified 25 EFS indicators in 37 lake-edge wetlands consisting of 12 peatlands, 8 alder swamps, and 17 ash swamps. We analyzed the synergies and trade-offs among wetland types and among EFS indicators, as well as the general EFS provisioning patterns of each type using cosine similarities and multivariate analysis. We showed that wetland type strongly influences the strength and direction of associations, with peatlands and ash swamps showing opposing patterns. While some EFS categories are less sensitive to indicator choice and aggregation, others, such as biodiversity, show important trade-offs. Our results revealed that synergies and trade-offs are strongly influenced by indicator choice and that protecting a diversity of wetland types is necessary to support multiple EFS categories.

1. Introduction

Wetlands provide numerous ecosystem functions and services (EFS) and are essential to human well-being. For instance, they improve water quality, control nutrient cycling, store water and carbon, limit erosion, support recreational and educational activities, and are biodiversity hotspots (Mitsch and Gosselink, 2000; Zedler, 2003; MEA, 2005). Despite these benefits, wetlands are among the ecosystems undergoing the most rapid and pervasive changes (Ramsar Convention on Wetlands, 2018). It is estimated that since the beginning of the 18th century, 87% of the area of wetlands on Earth has been lost (Davidson, 2014), mainly due to land conversion (MEA, 2005, Ramsar Convention on Wetlands, 2018), inadequate application of legislation (Poulin et al., 2016), and climate change (Erwin, 2009; Salimi et al., 2021).

Systematic conservation planning strategies aim to identify cost-efficient networks of conservation sites that that maximize EFS gains and minimize costs (Villarreal-Rosas et al., 2020; Cimon-Morin et al., 2021) or landscape multifunctionality (Bennett et al., 2009). Strategies based on landscape multifunctionality are optimal for such a task (Bennett et al., 2009), since they have the advantage of explicitly considering both synergies and trade-offs among EFS (Chan et al., 2006; Rodríguez et al., 2006; Bennett et al., 2009). Synergies occur when multiple EFS simultaneously increase, while trade-offs arise when the increase in one EFS happens at the cost of another (Raudsepp-Hearne et al., 2010). However, the strength and direction of EFS associations depend on the indicators chosen (Bennett et al., 2009; Cimon-Morin et al., 2013; Harrison et al., 2014) and may vary across regions (Jopke et al., 2014; Yang et al., 2014), spatial scale (Raudsepp-Hearne and Peterson, 2016), and ecosystem types (Lamy et al., 2016). For instance, in a study of synergies and trade-offs among multiple EFS provided by

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the Yangtze river delta in China, Yang et al. (2014) observed diverging association patterns between productivity and carbon sequestration depending on the indicators used: while tea production was in synergy with carbon sequestration, agricultural production and livestock breeding were rather in trade-off with this EFS.

Biodiversity is particularly sensitive to indicator choice and aggregation, as it can be quantified using different taxa and approaches. Synergies among taxa are uncommon and, as is the case for other EFS, depend on spatial scale, regional and climatic history, and ecosystem types (Wolters et al. 2006; Tisseuil et al., 2013). Since the acquisition of primary data on biodiversity requires expertise, time, and monetary resources, proxies such as land-use cover (Chan et al., 2006; Maes et al., 2012) or information gathered from other studies (Turner et al., 2007; Naidoo et al., 2008) are often used instead. However, aggregating biodiversity variables or choosing a single taxonomic group may mask meaningful associations. For instance, Hansson et al. (2005) studied the associations between nutrient retention and various biodiversity metrics in wetlands. They observed synergies with bird richness, trade-offs with benthic invertebrate richness and no association with plant richness. Ignoring such differences could lead to flawed decisions in landscape management (Plummer, 2009; Eigenbrod et al., 2010).

Wetlands present a variety of hydrologic, edaphic, and vegetal characteristics, which support a wide array of EFS (MEA, 2005). They also participate in the EFS provisioning of lacustrine systems, as they contribute to, for example, water quality, erosion control, carbon storage, and biodiversity (Kansiime et al., 2007; Sierszen et al., 2012; Cooper et al., 2014; Yang et al., 2018; Dubois et al., 2020). While we usually group them under a single term, lake-edge wetlands are highly diverse systems that are shaped by hydrogeomorphological variables, such as water level, slope, and hydroperiod (Lemein et al., 2017; Loiselle et al., 2021). As such, we still know very little about the quantitative differences in EFS provisioning among wetland types, as most studies on EFS in wetlands either aggregate sites into a single category (Hansson et al., 2005; Jessop et al., 2015; Varin et al., 2019, but see Zauft et al., 2010; Magnan et al., 2020), examine only one wetland type (Birol and Cox, 2007; Acreman et al., 2011; Doherty et al., 2014; Yang et al., 2018), or quantify a single EFS (Breaux et al., 1995; Costanza et al., 2021). Since EFS are quantified using similar indicators as those used to classify wetlands, important differences can be expected, but have yet to be quantified, and are rather based on "expert knowledge". To optimize conservation planning, a detailed portrait of synergies and trade-offs in different types of wetlands should cover many EFS using several indicators at a high level of spatial resolution. Moreover, studies investigating EFS synergies and trade-offs in wetlands are mostly centered on restored or constructed systems (Hansson et al., 2005; Doherty et al., 2014; Jessop et al., 2015). Thus, a better understanding of EFS trade-offs and synergies among wetland types in systems not impacted by human activities would provide a baseline for conservation in the face of climate and land-use changes. Such reference scenarios are essential to assess impacts and prioritize restoration efforts.

This study explored synergies and trade-offs in three types of lake-edge wetlands and among a wide range of EFS indicators, with a particular focus on biodiversity. We addressed the following questions: 1) in what ways do EFS provided by three types of lake-edge wetlands differ, and 2) how are the synergies and trade-offs among EFS affected by ecosystem types, indicator choice, and aggregation? To answer these questions, we quantified 25 indicators of eight different EFS in 37 wetlands situated along the shore of a medium-sized southern boreal lake and subjected to low levels of anthropogenic activity. Among those indicators, eleven were directly related to biodiversity. We then implemented multivariate analyses and cosine similarities to compare synergies and trade-offs among EFS indicators across the three wetland types. We hypothesized that different lake-edge wetland types support contrasting EFS and that biodiversity indicators show particularly strong trade-offs.

2. Methods

2.1. Study area

We conducted this study on lake-edge wetlands located along the shore of Lake Papineau (Fig. 1), a 12.9 km^2 boreal lake (11.2 km length; 3.4 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 lake receives water from runoffs (76%), direct precipitation (18%), and groundwater inflow (6%) (Harris et al., unpubl. data), and discharges from a single outlet as the source of the Kinonge (Salmon) river, flowing southward into the Ottawa River (Larocque, unpubl. data). Lake Papineau's watershed (93.5 km^2) is located at the southern limit of the sugar maple-yellow birch bioclimatic region. The lake itself constitutes 14 % of the watershed area, while the rest is composed of woodlands (72 %), wetlands (10 %), and other small lakes (4 %).

Most of Lake Papineau and its watershed (77 % and 66 %, respectively) are located within the private fish and game reserve Kenauk Nature. The long-term vision for managing this territory is to harmonize recreation, conservation, research, and logging activities. Housing density around the lake remains low (0.5 cottages per kilometer of shoreline), and other human disturbances, such as roads and agriculture, are almost nonexistent in the watershed. Before 2006, intensive logging activities, such as strips of clear-cutting, were conducted in certain areas of the watershed, which have since been replaced by more sustainable forest management practices that better protect the soil and are conducive to forest regeneration.

2.2. Site selection

In the summer of 2018, we conducted an exhaustive systematic survey by boat along the shores of Lake Papineau to identify all existing lake-edge wetland sites. We defined lake-edge wetlands as ecosystems where hydromorphic soil and hydrophilic vegetation are present along the edges of the lake but clearly distinct from it. Therefore, we did not consider submerged and floating aquatic plant beds in our sampling. All lake-edge wetlands were then classified and delineated in the field with a GPS using hydrological, pedological, topographical, and botanical characteristics (Lachance et al., 2021; Dubois et al., 2020; Appendix D). All wetlands are partially flooded after snowmelt and small water channels and ponds remain visible in a majority of sites throughout the summer. Peatlands (mostly poor fen), often consisting of floating mats, were dominated by short ericaceous shrubs and *Sphagnum* mosses. Alder swamps were dominated by dense thickets of speckled alder shrubs. Ash swamps were dominated by black ash, with tree cover reaching at least 30 %. Although we identified two emergent herbaceous marshes, they were not sampled due to their small number. We sampled all peatlands (12) and alder swamps (8), and a subset of ash swamps (17) Although the 37 sampled wetlands are connected to the same lake, the intricacies of the lake shape greatly lower the connectivity among its different basins (Fig. 1). However, we ensured that the sampling ash swamps were uniformly distributed among all parts of the lake.

2.3. Selection of ecosystem functions and services and their indicators

We selected eight EFS categories to account for all the concerns expressed by stakeholders in this project: biodiversity, support to pollinators, erosion control, water regulation, carbon storage, fishing, recreation, and aestheticism (Table 1). Then, we identified and quantified 25 indicators related to those EFS, which were used to quantify the synergies and trade-offs among EFS. The stakeholders identified biodiversity as one of the most important EFS. Therefore, we quantified plant, bird, fish, zooplankton, and singing orthopterans richness in all sites, as well as functional diversity of the first four taxa, at-risk species abundance, and habitat diversity. We quantified support for pollination

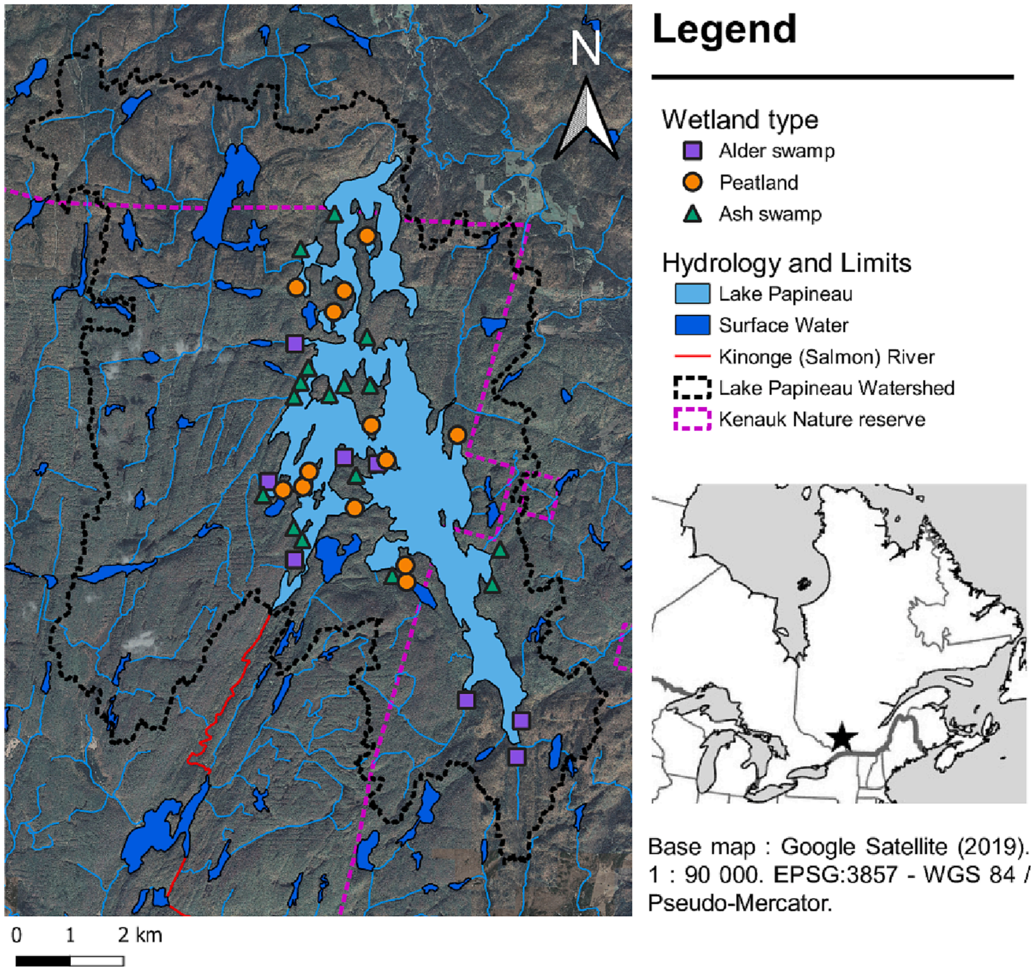

Fig. 1. Geographic situation of the 37 lake-edge wetlands located along the shores of Lake Papineau, Québec, Canada, and the site's hydrological context.

through an assessment of the floral resource available to pollinators, whereas we quantified fishing activities through fish abundance and availability of fish habitats. We associated indicators influencing sediment retention and wave-energy attenuation by the vegetation to the EFS erosion control and indicators affecting water storage, quality, and residence time of water coming from the watershed to the EFS water regulation. We also assessed carbon stocks in both above- and belowground compartments in all wetlands. We considered the EFS category recreation through indicators of site accessibility and the reciprocal of stinging insect abundance. Finally, we associated aestheticism with indicators of visual appeal, i.e., low shoreline vegetation allowing for an unobstructed view and the length of the site perimeter visible from the lake.

We refined the selection of indicator variables using the following criteria: 1) relevance for the study area; 2) scale, availability, and quality of the data; 3) possibility to acquire the data if not already available; 4) degree to which the literature justifies the use of an indicator; and 5) degree of mutual exclusivity (Varin et al., 2019). Since some indicators are used to quantify more than one EFS in the literature, we accounted for every documented association (Table 1). We chose at least two indicators for each EFS. Because one of our objectives was to investigate the impact of indicator choice and aggregation on synergies and trade-offs, we conserved all the selected indicators (25) in subsequent analyses. This allowed us to identify potential differences in association patterns among indicators within a given EFS category. The methods used to quantify the indicators, and justifications of their associations with the different EFS, are presented in Appendix A.

2.4. Statistical analysis

To analyze EFS synergies and trade-offs among the three wetland types, we first performed a principal coordinate analysis (PCoA) on a Gower dissimilarity matrix containing the 25 EFS indicators for the 37 sampled wetlands (Legendre and Legendre, 2012). The matrix was standardized to z-scores ($\mu = 0$ and $\sigma = 1$) to give equal weight to all indicators (Lavorel et al., 2011). This allowed computing the dissimilarity between each site according to the value of their EFS indicators in n dimensions, where n is the number of EFS indicators. For each site, coordinates of n dimensions (i.e., site scores) are generated to indicate its position in the multivariate space. Next, we used the Broken Stick model to estimate the number of statistically significant principal coordinates (Jackson, 1993; Legendre and Legendre, 2012). We used the site scores of the significant principal coordinates to compute the centroid for each wetland type.

We quantified synergies and trade-offs between wetland types and indicators by calculating cosine similarities between the three wetland type centroids and the 25 indicator vectors from the PCoA. Cosine similarity calculates the cosine of the angle between two vectors of n dimensions (Satya and Murthy, 2012). More precisely, it corresponds to the scalar product of two vectors divided by the product of their lengths. Cosine similarities can range dorm -1 (180° angle: high dissimilarity) to $+1$ (0° angle: high similarity). This method is well suited to investigate multifunctionality. Instead of looking at each interaction pair independently through linear correlations, we can quantify interactions in the n dimensions of the PCoA. We also calculated cosine similarities between all indicators as well as between the 37 sites and the 25 indicators.

Table 1
Ecosystem functions and services (EFS) indicators quantified in three types of lake-edge wetlands located along the shores of Lake Papineau, Québec, Canada. See Appendix A for more details on each indicator. The two last columns respectively present the EFS category associated with each indicator and the sources from the literature supporting this association.

EFS indicator	Code	Description	EFS categories	Sources
Biotic indicators				
Plant richness	plant_rich	Number of vascular plant species sampled	Biodiversity	Anderson et al., 2009; Egoh et al., 2009
Bird richness	bird_rich	Number of bird species sampled	Biodiversity	Anderson et al., 2009; Egoh et al., 2009
Fish richness	fish_rich	Number of fish species sampled	Biodiversity	Worm et al., 2006; Lindegren et al., 2018
Zooplankton richness	zoo_rich	Number of zooplankton taxa sampled	Biodiversity	Worm et al., 2006
Singing orthopterans richness	sing_rich	Number of singing orthopterans species sampled	Biodiversity	
Plant functional diversity	plant_fd	Plant functional diversity calculated with functional dispersion	Biodiversity	de Bello et al., 2010; Lavorel et al., 2011
Bird functional diversity	bird_fd	Bird functional diversity calculated with functional dispersion	Biodiversity	
Fish functional diversity	fish_fd	Fish functional diversity calculated with functional dispersion	Biodiversity	Lindegren et al., 2018
Zooplankton functional diversity	zoo_fd	Zooplankton functional diversity calculated with functional dispersion	Biodiversity	
Habitat diversity	habitat_div	Shannon diversity index of land cover categories within the site	Biodiversity / Aestheticism	Maes et al., 2012; Dramstad et al., 2006; Harrison et al., 2014
At-risk species	risk_sp	At-risk species index calculated using the protection status of plant, bird and fish species in Quebec, Canada	Biodiversity	Egoh et al., 2009; Eigenbrod et al., 2010; Burkhard et al., 2012
Floral divergence	flower_div	Standard deviation of plant communities' flowering period	Support to pollinators	Lavorel et al., 2011
Biotic pollination	pol_bio	Index based on number of plant species pollinated by insects and animals	Support to pollinators	Maskell et al., 2013; Schulp et al., 2014
Fish abundance	fish_abund	Catch per unit effort of fish within the site	Fishing	Hein et al., 2006; de Bello et al., 2010; Harrison et al., 2014
Stinging insects scarcity	sting_scarc	1 / Number of stinging insects caught	Recreation	Boughton et al., 2019
Abiotic indicators				
Site to sub-watershed ratio	site_ratio	Ratio of site area (m^2) on area of the sub-watershed of the site (m^2)	Water regulation	Mitsch and Gosselink, 2000
Site to surface water ratio	wet_ratio	Ratio of site area (m^2) on total wetland and open waters area in the sub-watershed (m^2)	Water regulation	Mitsch and Gosselink, 2000
Water cover	water_cover	Total area in the site covered by open water (m^2)	Water regulation / Fishing	De Laune and Reddy, 2008; de Groot et al., 2010
Site flatness	site_flatness	1 / Mean slope in the site (%)	Water regulation / Erosion control	Mitsch and Gosselink, 2000; Madsen et al., 2001; De Laune and Reddy, 2008; Nedkov and Burkhard, 2012
Soil organic carbon content	soil_C	Organic carbon content of the topsoil (%)	Carbon storage / Water regulation	Bridgham et al., 2006; Egoh et al., 2009; Zauft et al., 2010; Price, 2011; Magnan et al., 2020
Above-ground carbon	above_C	Carbon stock (kg) in above-ground canopy of the site	Carbon storage	Bridgham et al., 2006; Egoh et al., 2008; de Bello et al., 2010; Zauft et al., 2010; de Groot et al., 2010; Davies et al., 2011; Magnan et al., 2020
Terrestrial access to site	access_land	Accessibility index, by terrestrial means,	Recreation	Martínez-Harms and Balvanera, 2012
Nautical access to site	access_water	Accessibility index, by nautical means,	Recreation	Martínez-Harms and Balvanera, 2012
Riverine perimeter length	lake_perim	Length (m) of the site's perimeter connected to the lake	Erosion control / Aestheticism	de Groot et al., 2010
Riverine vegetation height	shore_vege	Mean height (m) of the site vegetation within a 10 m buffer zone along the shore of the lake	Erosion control / Aestheticism*	Egoh et al., 2008; Neary et al., 2009; de Bello et al., 2010; de Groot et al., 2010; Silliman et al., 2019

We evaluated EFS patterns among wetland types using a 0.75 threshold on the cosine similarities between wetland centroids and each indicator. A wetland type supported a category of EFS if at least one of its indicators had a cosine similarity with the centroid of ≥0.75. We chose this threshold because it allowed for a clear separation of our indicators. At a lower cosine similarity threshold, all wetland types supported all EFS. At a higher threshold, some wetland types did not support any EFS. We repeated the above procedure on all 37 sites. We performed all statistical analyses in R 4.1.1 (R Core Team, 2021). We used packages "ape" (Paradis and Schliep, 2019) and "vegan" (Oksanen et al., 2020) to compute the PCoa, "cluster" (Maechler et al., 2021) to compute the Gower distance matrix, "ClassDiscovery" (Coombes 2021) and "PCDimension" (Coombes and Wang, 2019) to compute the Broken stick model and "lsa" (Wild, 2020) to compute the Cosine similarities.

3. Results

The three first PCoA axes were retained according to the Broken stick criteria and accounted for 71 % of the total explained variation among sites. The first axis (PC1) explained 39.8 % of the variation and clearly distinguished the three wetland types (Fig. 2), with peatlands and ash swamps located at opposite sides of the axis. This axis was mainly associated with EFS indicators of carbon storage, shoreline vegetation, and length, as well as the diversity of plants, birds, zooplankton, and singing orthopterans. The other two axes (PC2 and PC3) explained 18.9 % and 13.4 % of the variation, respectively, and they are both mainly associated with indicators of hydrogeomorphology (e.g., site_ratio and wet_ratio) and of fish diversity and abundance (Fig. 2).

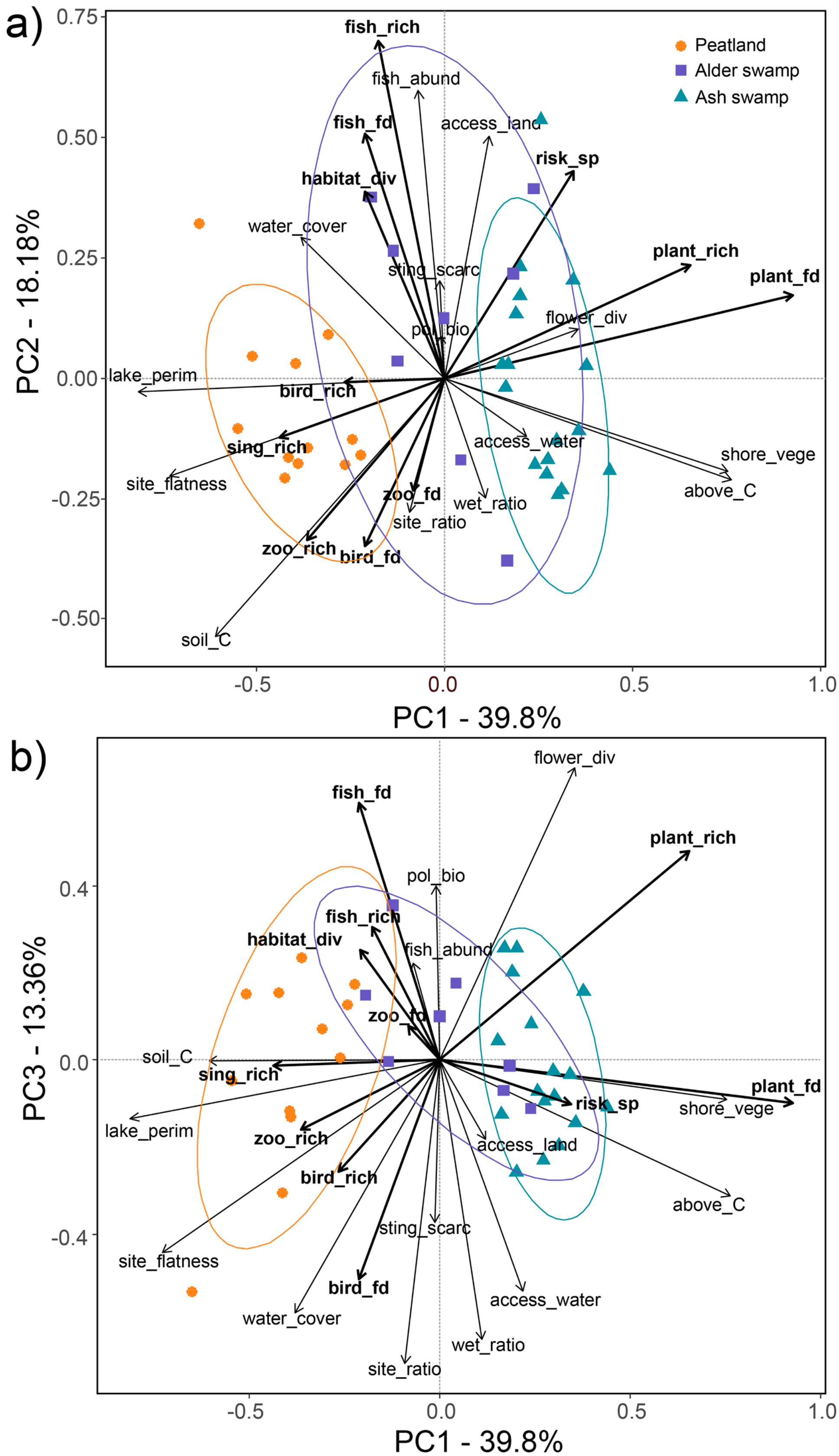

Fig. 2. Principal coordinate analysis (PCoA) of EFS indicators for the three types of wetlands studied. Panel a) shows principal coordinates one and two and panel b) shows principal coordinates one and three. See Table 1 for indicator code description.

3.1. Synergies and trade-offs among wetland types

Cosine similarities between wetland centroids and indicators exhibited divergent patterns among wetland types (Table 2). Peatlands were in synergy with singing orthopterans richness, short shoreline vegetation, long lake perimeter, flat terrain, high organic matter content in the soil, as well as zooplankton and bird richness. Ash swamps were mainly associated with plant richness and functional diversity, tall shoreline vegetation, and large above-ground carbon stocks. Peatlands and alder swamps showed general trade-offs, as they were associated with opposite indicators. Alder swamps were mainly associated with the abundance, richness, and functional diversity of fish, as well as a high diversity of habitats.

3.2. Synergies and trade-offs among EFS indicators

Some EFS showed strong synergies among their indicators, while others presented a mix of trade-offs and synergies (Fig. 2). Biodiversity indicators exhibited considerable variability in cosine similarities. Richness and functional diversity indicators were in synergy for all sampled taxa. Inter-taxa synergies were observed between bird, zooplankton, and singing orthopterans indicators, as well as between plant and fish indicators. However, almost all other interactions between richness and functional diversity indicators constituted trade-offs. Habitat diversity was in strong synergy with fish richness and functional diversity but presented substantial trade-offs with plant, bird, and zooplankton functional diversity, as well as bird and zooplankton richness. The abundance of rare species was in synergy with plant and fish richness in addition to plant functional diversity. Still, it showed trade-offs with the richness of birds, zooplankton, and singing orthopterans and with birds and zooplankton functional diversity.

We observed synergies for all pairs of indicators characterizing support to pollinators, water regulation, fishing, recreation, and aestheticism (Appendix B). On the contrary, erosion control showed mixed patterns of synergies and trade-offs among pairs of indicators. As for carbon storage, there was a clear trade-off between above- and

Table 2
Cosine similarities between the centroid of each wetland type and each EFS indicator vector from the principal coordinate analysis (PCoA). Column "EFS category" presents EFS associated with each indicator, and colors indicate the strength and direction of the cosine similarity, with strong positive similarities in dark blue and strong negative similarities in dark red. For the EFS category of Aestheticism, the sign of the cosine similarity of indicator shore_vege should be inverted since taller vegetation along the shoreline decreases visual appreciation. See Appendix A for further details.

Indicators	Peatlands	Alder swamps	Ash swamps	EFS category
sing_rich	0,99	-0,41	-0,95	**Biodiversity**
lake_perim	0,98	-0,29	-0,97	Erosion control / Aestheticism
site_flatness	0,88	-0,61	-0,78	Water regulation / Erosion control
soil_C	0,84	-0,67	-0,73	Carbon storage / Water regulation
zoo_rich	0,81	-0,82	-0,66	**Biodiversity**
bird_rich	0,74	-0,52	-0,66	**Biodiversity**
water_cover	0,47	-0,19	-0,45	Water regulation / Fishing
zoo_fd	0,45	-0,63	-0,32	**Biodiversity**
bird_fd	0,44	-0,92	-0,25	**Biodiversity**
habitat_div	0,26	0,83	-0,47	**Biodiversity** / Aestheticism
site_ratio	0,22	-0,83	-0,04	Water regulation
fish_fd	0,13	0,87	-0,34	**Biodiversity**
fish_rich	0,06	0,91	-0,28	**Biodiversity**
sting_scarc	-0,01	-0,10	0,03	Recreation
pol_bio	-0,05	0,71	-0,11	Support to pollinators
fish_abund	-0,05	0,93	-0,16	Fishing
wet_ratio	-0,06	-0,77	0,24	Water regulation
access_water	-0,30	-0,60	0,45	Recreation
access_land	-0,35	0,60	0,23	Recreation
flower_div	-0,52	0,67	0,39	Support to pollinators
risk_sp	-0,72	0,64	0,61	**Biodiversity**
above_C	-0,83	-0,25	0,93	Carbon storage / Erosion control
plant_rich	-0,83	0,67	0,72	**Biodiversity**
shore_vege	-0,91	-0,10	0,97	Erosion control / Aestheticism*
plant_fd	-0,99	0,26	0,98	**Biodiversity**

below-ground carbon stocks.

3.3. Patterns of EFS provisioning among wetland types

All three types of wetlands strongly supported EFS biodiversity (Table 3; Appendix C). Peatlands specifically supported four additional EFS: erosion control, water regulation, carbon storage, and aestheticism. Alder swamps supported fishing and aestheticism. Finally, ash swamps supported erosion control and carbon storage.

4. Discussion

The study of landscape multifunctionality through the synergies and trade-offs of indicator variables provides an integrative portrait of EFS provisioning (Bennett et al., 2009). In wetlands, the few studies that explored such synergies and trade-offs did not compare wetland types, targeted mainly constructed or restored systems, studied a limited number of indicators and EFS, and often used proxy-based assessment methods (Hansson et al., 2005; Doherty et al., 2014; Jessop et al., 2015; Yang et al., 2018). To the best of our knowledge, our work is the first to compare EFS provisioning among multiple wetland types, quantify multiple indicators to study several EFS categories, and use high-–resolution *in situ* data on wetlands subjected to low levels of anthropogenic activity. Our results provide the first empirical evidence that wetland typology influences EFS provisioning, with peatlands and ash swamps associated with contrasted indicators. Furthermore, biodiversity is the EFS category that exhibited the most trade-offs among its indicators.

4.1. Synergies and trade-offs among wetland types

Wetland types were associated with different sets of indicators and supported distinct EFS categories. We expected these results, as EFS quantification relies on indicators similar to those typically used to classify wetlands (Loiselle et al., 2021). In particular, peatlands and ash swamps were almost mirror opposites regarding their specific indicators. Nevertheless, our results showed that the different wetland types could support the same EFS through different indicators. For instance, peatlands maximize carbon storage in their soil, while ash swamps maximized it in aboveground plant tissues. Furthermore, the flat slope and long riverine perimeter of peatlands are factors increasing shoreline stability against erosion (Gacia and Duarte, 2001; Feagin et al., 2011), while in ash swamps, it can be related to the tall stature of the vegetation (Neary et al., 2009; Silliman et al., 2019). Different indicators of carbon storage and erosion control often underline different processes that must not be aggregated in EFS studies. Our results suggest that trade-offs among EFS categories become apparent whenever we increase the number of indicators used or land-cover types considered. While this conclusion may seem obvious, it underlines the dynamic nature of EFS associations, and thus of any management plan that would rely on these.

Indicators within EFS categories of support to pollinators, fishing, water regulation, recreation, and aestheticism of lake-shore wetlands all showed synergies among each other. Support to pollinators and fishing categories were each represented by two indicators that often covary positively. These indicators were the incidence of nectar-producing plant species and the seasonal abundance of resources for pollinators, and the abundance of fish and the availability of habitats. Thus, trade-offs may emerge by including different indicators, such as the diversity of pollinators, or the abundance of fish prey, for example. The other EFS categories (i.e., water regulation, recreation, aestheticism) were described by indirect proxies, such as wetland area, plant stature, and perimeter length, which could artificially induce synergies. The measurement of field-based indicators, such as water flow monitoring or habitat use by the large fauna, may have revealed trade-offs. Hence, the evaluation of EFS provisioning is highly contingent on our choice of indicators and that trade-offs are expected to accumulate by increasing the number of indicators.

Table 3
Ecosystem functions and services (EFS) provided by the three wetland types studied. Boxes marked with an X identify EFS for which at least one indicator had a cosine similarity of $\geq$0.75.

EFS	Peatlands	Alder swamps	Ash swamps
Biodiversity	X	X	X
Support to pollinators			
Erosion control	X		X
Water regulation	X		
Carbon storage	X		X
Fishing		X	
Recreation			
Aestheticism	X	X	

4.2. Biodiversity among wetland types

Our results emphasize diverging patterns among wetland types for the biodiversity indicators. Ash swamps were mainly associated with plant diversity, alder swamps supported fish diversity, while peatlands supported birds, singing orthopterans, and zooplankton diversity. Furthermore, all three wetland types maximized different dimensions of biodiversity. Those differences are rarely quantified, and our results further stress the potential impacts of indicator choice of EFS quantification. If only one taxonomic group is used as an indicator of diversity, important trade-offs could arise for other taxa. Inclusion of other indicator taxa (dragonflies, salamanders, benthic and soil organisms) would likely not change the overall conclusion, which is that there are strong trade-offs among biodiversity variables between wetland types.

Plant richness and functional diversity were the highest in ash swamps, likely due to the hydrological gradient associated with their steeper slope (i.e., low elevation values near the shore and high elevation values far from the shore). Dry conditions at higher elevations in ash swamps favor the presence of upland species, therefore increasing overall plant diversity (Dubois et al., 2020). At-risk species abundance can also be explained by hydrological variations, as five of the seven at-risk species were plants associated with upland habitats and were mainly found in ash swamps. On the other hand, alder swamps were mostly associated with fish biodiversity and the presence of two at-risk fish species (*Ameiurus natalis* and *Notropis bifrenatus*). The presence of beaver ponds and small streams in alder swamps increases the hydrological connectivity and the diversity of fish habitats (Jude and Pappas, 1992; Langer et al., 2018).

Peatlands showed the greatest bird, singing orthopterans, and zooplankton diversity. Bird diversity in wetlands is typically associated with high habitat diversity (Desgranges et al., 2006), large patches of vegetation (Keller et al., 1993; Hansson et al., 2005), the presence of standing water (Grover and Baldassarre, 1995), and the availability of foraging resources (Gawlik, 2002; Carlos et al., 2017). In our study, while habitat diversity was higher in alder swamps, peatland patches were larger, had a greater open water cover, and supported a higher abundance of fruiting shrubs (Appendix A). Singing orthopterans generally favor open habitats dominated by grasses (Bidau, 2014), and were found in abundance within peatlands, but were relatively scarce in swamps. However, the probability of detecting bird or insect species might have been lightly biased methodologically due to the acoustic range covered by the microphones used (ca. 50–100 m radius depending on weather conditions and species) and the presence of upland forests near the study sites. Nevertheless, these biases were likely similar between the wetland types.

While associations among biodiversity indicators were generally variable, the richness and functional diversities of each taxon were always in synergy. The positive association between richness and functional diversity has been observed in other studies (Petchey and Gaston, 2002; Heino, 2008; Suárez-Castro et al., 2022). Yet, factors such as ecosystem type (Biswas and Mallik, 2010; Morelli et al., 2018) and disturbance intensity (Flynn et al., 2009; Mouillot et al., 2013) are associated with trade-offs. As such, even though we found synergies between richness and functional diversity, the use of one as a surrogate for the other in EFS studies should be considered with prudence, especially when conducted in disturbed areas.

4.3. Conclusion

Studies that rely on multivariate approaches to characterize wetland multifunctionality have been centered on a limited number of EFS in a single wetland type of constructed or restored systems (Hansson et al., 2005; Doherty et al., 2014; Jessop et al., 2015; Yang et al., 2018). In the present study, we used multiple indicators calculated mainly from high-resolution primary data to quantify eight EFS in 37 wetlands of three different types. This approach allowed the detection of synergies and trade-offs among indicators within each EFS category without information loss by omission, aggregation, or low-resolution data. We showed that synergies and trade-offs are strongly influenced by both indicator choice and aggregation, stressing the need for thought-through methodological choices in EFS studies that reflect the processes of interest and the stakeholder's concern.

While differences in EFS provisioning among wetland types are generally assumed or based on "expert knowledge", our study is the first to quantify those differences for multiple EFS using a large array of indicator variables. Our study is also one of the first to evaluate both the aquatic (fish and zooplankton) and terrestrial (birds and singing orthopterans) components of wetland biodiversity. These two components show no clear associations and capture different dimensions of biodiversity. These findings emphasize the potential pitfalls of conservation measures targeted at aggregated measures of biodiversity. Our results also provide a benchmark for conservation planning, as they offer an extensive portrait of the synergies and trade-offs among the EFS of wetlands that are subjected to low levels of anthropogenic disturbances. While synergies and trade-offs may be pervasive both within and between EFS categories, as well as between wetland types, they are also influenced by external drivers, such as invasive species, climate and land-cover changes. We do not know how anthropogenic activities might impact the balance between trade-offs and synergies, which can only be assessed by establishing proper reference conditions, as we have done in this study.

CRediT authorship contribution statement

Audréanne Loiselle: Conceptualization, Data curation, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. **Raphaël Proulx:** Conceptualization, Funding acquisition, Methodology, Resources, Supervision, Validation, Writing – review & editing. **Marie Larocque:** Conceptualization, Funding acquisition, Writing – review & editing. **Stéphanie Pellerin:** Conceptualization, Funding acquisition, Methodology, Resources, Project administration, Supervision, Validation, Writing – review & editing.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Appendix A contains supplementary methods concerning indicator quantification, and supplementary tables S1-9. Appendix B contains cosine similarity matrix of EFS indicators. Appendix C contains a synthesis of EFS provided by the 37 sampled wetlands. Appendix D contains photographs of each type of wetland sampled. Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2023.110547.

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