




ARTICLE

Freshwater fish sanctuaries provide benefits for riparian wildlife

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Abstract

Benefits to wildlife communities stemming from the protection of a single species have been documented in terrestrial and marine systems but remain understudied within the context of freshwater-protected areas (FPAs). We used five long-standing (>80 years) FPAs in three lakes in eastern Ontario, Canada, which were initially established to protect native black bass (*Micropterus* spp.) from angling exploitation, to assess whether this protection affected wildlife communities found in the riparian areas of these FPAs. From May to July 2021, we used baited remote camera traps and visual surveys to assess species diversity within and outside of FPAs. We recorded 61 species spanning mammalian, avian and herpetofauna taxa, with the two assessment methods identifying unique sets of species (23% overlap). Camera traps showed that animals were more active in riparian areas during the day (62% of detections) than at night. FPAs had a variable but overall positive influence on riparian wildlife biodiversity, hosting more bird, mammal, amphibian and reptile species than non-protected areas and having higher species richness. FPAs differed from other sites in the lakes by having higher habitat complexity, less human infrastructure and less human use, which potentially contributed to these differences. This study raises awareness that even small FPAs can have legacy, umbrella-type benefits that extend beyond fishes to the wildlife that use the adjacent riparian areas.

KEYWORDS

biodiversity, freshwater lakes, habitat, protected areas, shoreline, umbrella species

1 | INTRODUCTION

Biodiversity is a central pillar in supporting the health of ecosystems and the continuation of their functions (Sayer et al., 2021; Srivastava & Vellend, 2005). However, the diversity of natural communities is being lost at an increasing rate severe enough for the declaration of

a biodiversity crisis (Singh, 2002). The emergence and intensification of new environmental stressors such as climate change and anthropogenic habitat loss have accelerated the degradation of ecosystems with such impacts being particularly evident in freshwater systems (Albert et al., 2021; Harrison et al., 2018; Reid et al., 2019). One of the greatest threats to freshwater biodiversity is the

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degradation of riparian areas, which commonly occurs as a direct result of shoreline development (Cooke et al., 2022). Riparian areas provide important connections between terrestrial and freshwater ecosystems, such that the loss of this habitat can impact biodiversity in both habitats (Krause et al., 2017; Naiman et al., 2010). It is well established that ecosystems with higher biodiversity are more resilient to biotic and abiotic stressors such as invasive species, diseases, habitat disturbances and climate change (Oliver et al., 2015). The conservation of freshwater biodiversity is critical for securing their resiliency in a changing world (Albert et al., 2021), and ambitious efforts are needed to halt freshwater biodiversity losses (Tickner et al., 2020; Twardek et al., 2021).

One strategy used to maintain or restore freshwater biodiversity is spatial conservation and management measures, commonly in the form of freshwater protected areas (FPAs). This can be achieved through mandating that species and resources found within portions of the landscape are not subjected to exploitation (Cooke et al., *In Press*), or that habitat is not lost to land conversion (Acreman et al., 2020). By minimizing anthropogenic pressures, these areas can maintain biodiversity and restore natural ecosystem processes in degraded areas (Abell et al., 2007; Hansen & DeFries, 2007), leading to the recovery of various aquatic species (Acreman et al., 2020; Hedges et al., 2010). FPAs may also be established to protect a specific species or group of species. Often called 'sanctuaries,' their design and management can be tailored to meet specific management goals (Suski & Cooke, 2007). In North America, this approach is most common for fish species, where sanctuaries are implemented to prevent the mortality of gamefish due to recreational fishing. Protection of a species and its habitat can lead to an unintended effect whereby non-target species both within and near the protected area also benefit. This effect is most likely to influence transition zones, including the riparian zone, that facilitate species interactions such as predator-prey dynamics (Krause et al., 2017). Here, many species depend on the interaction between aquatic and terrestrial habitats to support their lifecycle and thus may be impacted by alterations to either of these habitats. Moreover, these transition zones have the potential to support disproportionately high biodiversity and productivity (Naiman et al., 2010).

In this study, we assessed the riparian shorelines of three freshwater lakes in eastern Ontario (Canada) which contain five FPAs designated as provincial fish sanctuaries (no fishing all year). These areas have a longstanding protected status, as they were established approximately 80 years ago (in the 1940s) with the intention of protecting breeding habitat to support a highly valuable recreational fishery for native black bass (*Micropterus* spp.) with a particular focus on largemouth bass (*M. nigricans*). These FPAs support greater abundance and biomass of largemouth bass and shiners (golden shiner *Notemigonus crysoleucas*, common shiner *Luxilus comutus*, blackchin shiner *Notropis heterodon* and blacknose shiner *Notropis heterolepis*) within their borders (Zoldero et al., 2019). This motivated us to investigate whether similar umbrella effects were occurring for the broader wildlife communities found in the riparian areas within these fish sanctuaries. We predicted that riparian areas within FPAs would have higher wildlife diversity than other riparian areas in a lake.

2 | METHODS

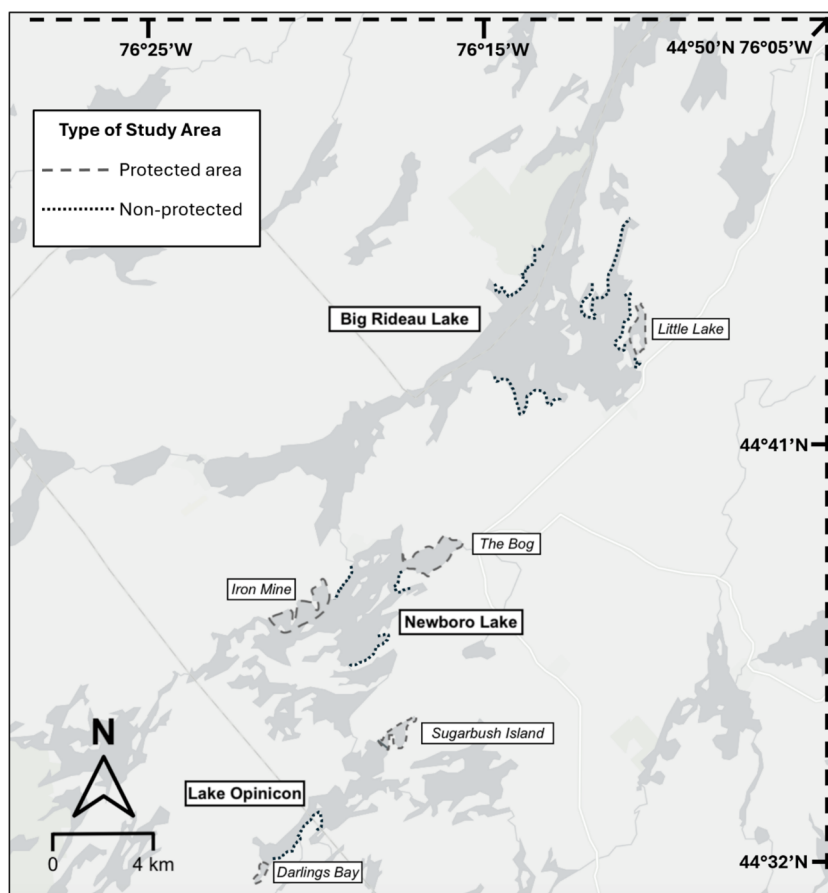
During the summer of 2021, biodiversity assessments were conducted on the shorelines of Big Rideau Lake (May 24–June 8), Newboro Lake (June 11–25) and Lake Opinicon (June 28–July 16) within the Ontario Rideau lakes system (Figure 1). Each of these lakes has one or two long-established fish sanctuaries over 80 years old (two sanctuaries each in lakes Opinicon and Newboro, one in Big Rideau Lake) that have a minimum of 3 km of shoreline in largely undisturbed and unpopulated bays, in contrast to the more disturbed shorelines found outside the sanctuaries. Assessments were conducted with remote camera traps and visual surveys.

Remote camera traps were deployed following protocols established by previous biodiversity studies (Green et al., 2020) and were modelled off sampling methods used in a riparian study of scavenging behaviour (Etherington et al., 2023). Camera traps were used to target a range of animals interacting with riparian habitats and were placed in sites that appeared most accessible to a variety of wildlife (with a traversable understory or near game trails).

A camera array consisting of one to five cameras was deployed at each site. Each site in a sanctuary was temporally paired with a site in the same lake but outside a sanctuary, with one site sampled (camera array deployed) in each type of location per day. To the extent possible, we sampled sites outside sanctuaries that had a similar type of habitat to that within sanctuaries (with shallow, wetland-like habitat near the shore; Figure 2d,e). As this limited the distribution of usable sites outside sanctuaries, these were non-randomly distributed around the lakes, resulting in clusters (see Figure 1 for locations of clusters). A total of five sites (camera arrays) outside sanctuaries were temporally paired with five sites within each FPA, except for one pair on Newboro Lake (Iron Mine) which had only four sites per location. Big Rideau Lake, with only one FPA, received double the number (10) of temporally paired sites to enable comparisons among lakes. We initially maintained a minimum of 600 metres of shoreline between each site to reduce the chance of double-counting individuals.

Trail cameras (CamPark T45A and Stealth Cam QV12) were set to record 15-second video clips when they were motion-triggered (recording at 16mp/1080p and 12mp/720p, respectively). Each camera was placed in the water 1 metre from the shoreline when possible, otherwise, cameras were positioned near the waterline when in-water accessibility was limited. In all cases, cameras were secured by attaching them to a T-bar at a height of 1 metre with the camera oriented inland (Figure 2a). All trail cameras were baited using a freshly caught bluegill sunfish (*Lepomis macrochirus*) impaled on a stick (to limit rapid scavenging and improve species detection) placed on land 2 metres from the camera. Bluegill was caught the morning of deployment and was euthanized by cerebral percussion (approved under Carleton University animal care protocol number 119111, following CCAC guideline number 113 and Cooke Lab SOP #3). Camera arrays were deployed at each site for 24 hours, after which the array was moved at least 100 metres to reduce learning by scavengers, and baited with a fresh fish. Cameras were not deployed within 100 metres of shoreline distance from a cottage or dock, and

FIGURE 1 Map of the study area in Ontario, Canada depicting sanctuaries (long dashes) within Big Rideau Lake (Little Lake), Newboro Lake (The Bog and Iron Mine) and Lake Opinicon (Darlings Bay and Sugarbush Island). Short dashes indicate the areas where camera and visual surveys were clustered.



islands were not used. Due to the large study area and a limited number of cameras, shorter observation periods were used to obtain greater spatial coverage.

The duration of camera array deployment was balanced between locations by reducing the camera durations to match the minimum observation period from any camera deployed each day (an inside/outside FPA pair). This was necessary as deployment times were staggered and identical recording windows set by deployment and retrieval times could not be achieved in all cameras in each array. Sampling effort was also balanced between locations such that the minimum number of deployed cameras in one array was used to set the number of usable cameras in its corresponding pair. However, this resulted in slightly different camera durations and number of cameras among the five FPA-paired locations.

A total of 252 individual cameras in 58 arrays (sites) were used in this study, half of which were within protected areas and half of which were outside protected areas. Big Rideau Lake had 44 cameras in 10 arrays in each location (inside and outside Little Lake). Newboro Lake had 20 cameras in four arrays (Iron Mine) and 20 cameras in five arrays (The Bog) in each location, and Lake Opinicon had 22 cameras in five arrays (Darlings Bay) and 20 cameras in five arrays (Sugarbush Island) in each location. Observation periods for each camera ranged from 21 to 24 hours.

Visual biodiversity surveys were conducted in the same locations as camera arrays. Each visual survey consisted of a 15-minute boat

ride covering 300 metres of shoreline. Visual surveys were conducted during the day (but not during rain or strong winds) within 30 m of shore from a flat-bottom boat propelled by an electric trolling motor. Observations of birds, mammals and herptofauna were made by two researchers using 10x binoculars and included animals in trees, birds flying overhead, animals in the water on either side of the boat and birds identified by song. Thus, we use the term 'riparian' in a very loose sense. Four surveys were conducted per location (inside or outside an FPA, with the order alternated for each paired survey) and were also temporally paired as they were conducted on the same day, no more than three hours apart.

We generated species accumulation curves for each location, separated by assessment method. Species richness was based on summed species observations from all camera arrays or visual surveys. For camera arrays, most species had low numbers of individuals (<1 individual per camera array, on average, with two species that had higher numbers), and accurately identifying unique individuals was not possible. Thus, we did not use diversity metrics, but instead simply used the presence/absence of a species. For visual surveys, we are confident that each individual was only counted once during each survey, so here we used the Shannon diversity index.

Observations of individuals identified on cameras were categorized into day or night sightings (based on local sunrise/sunset time) and were compared between locations (inside and outside of FPAs) to assess whether there were differences in the daily use of these areas.

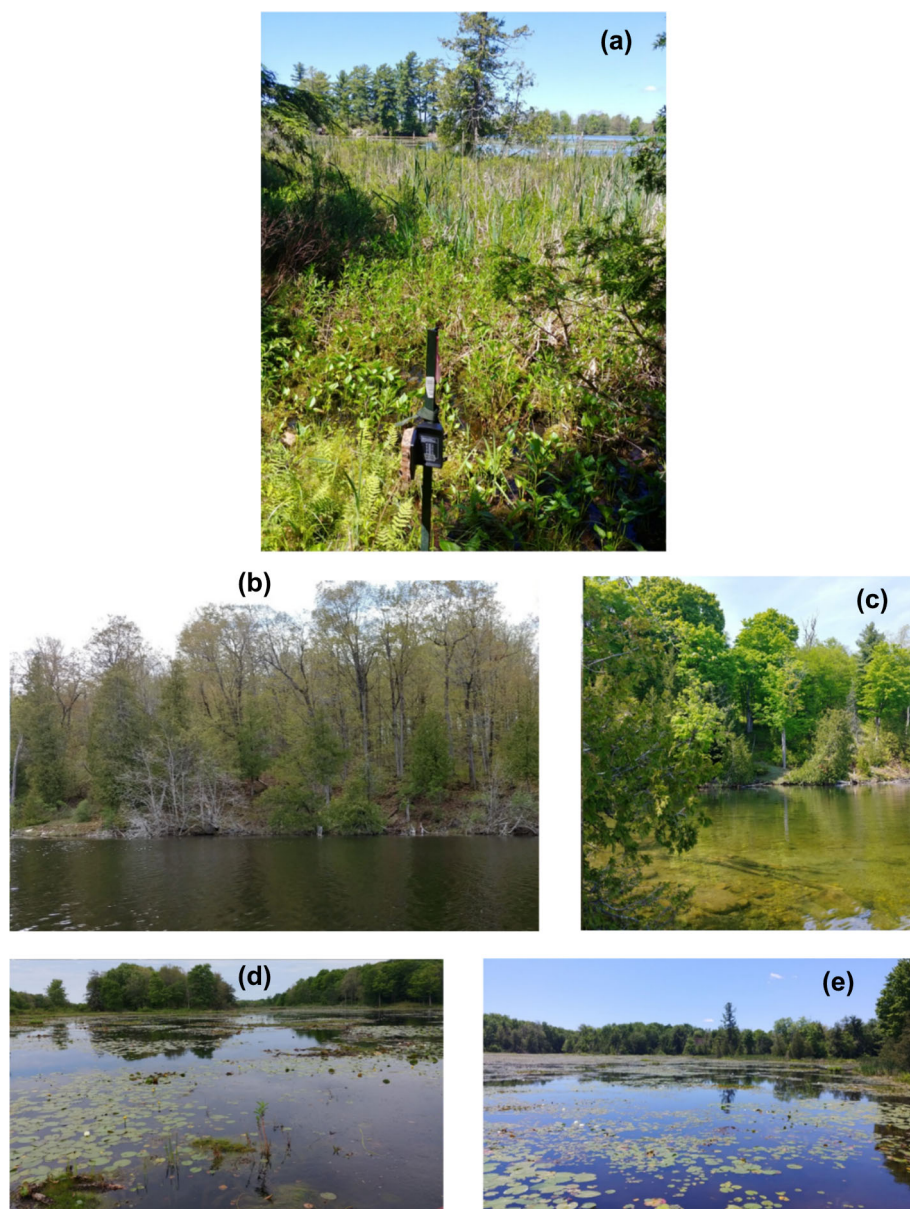


FIGURE 2 Examples of camera trap station study areas. (a) The Bog sanctuary on Newboro Lake with a cattail buffer between the lake and shoreline; (b) forested shoreline in Little Lake sanctuary on Big Rideau Lake; (c) comparable shoreline in the non-protected area of Big Rideau Lake; (d) shallow sediment-rich waters with extensive water lily cover in Iron Mine sanctuary of Newboro Lake; and (e) Little Lake sanctuary on Big Rideau Lake.

3 | RESULTS

In total, 61 species were detected. We indicated their status globally (<https://www.iucnredlist.org/>), in Canada (<https://laws.justice.gc.ca/eng/acts/s-15.3/page-10.html>) and in Ontario (<https://www.ontario.ca/page/species-risk-ontario>) in Table 1. The cameras detected a total of 29 species, while the visual surveys detected 46 species; 14 species were detected by both methods. We observed 37 species of birds, 17 species of mammal, 4 species of amphibians and 3 reptile species (Table 1, Figure 3). The species groups detected by both methods varied greatly, with mammals more commonly being detected by cameras than by visual surveys (17 vs. 5, respectively), while more bird (35 vs. 11), amphibian (4 vs. 0) and turtle (2 vs. 1) species were detected in visual surveys. Overall, more individuals (62%) were detected on camera traps during the day compared to at

night. During the daytime, more individuals were seen on cameras inside (67%) than outside (55%) the FPAs.

Fifty-four species were detected inside FPAs, while only 42 species were detected outside of them. Of those detected in only one type of location (26 species), 19 were only detected inside an FPA, while seven were only detected outside an FPA. Of the eight species listed provincially, federally, or globally, three occurred only inside an FPA (black tern *Chlidonias niger*, golden eagle *Aquila chrysaetos* and wood frog *Lithobates sylvaticus*), while one occurred only outside (wood thrush *Hylocichla mustelina*). Species accumulation curves showed that considerably more species were detected with visual surveys than with cameras (Figure 4a,b) and that both methods failed to plateau. However, when the number of arrays was doubled (summed by lake instead of by FPA), an asymptote was closer to being reached (Figure 4c,d).

TABLE 1 Summary of the species detected by two assessment methods (cameras or visual surveys), each species' status in three jurisdictions, and whether the species was detected inside or outside of a freshwater protected area (FPA). * denotes not native.

Species		Assessment method		Status			Detected	
Scientific name	Common name	Camera	Visual	Global	Canada	Ontario	Inside of an EPA	Outside of an FPA
Mammals								
<i>Castor canadensis</i>	American beaver	x		Least concern	Not listed	Not listed	y	y
<i>Neogale vison</i>	American mink	x	x	Least concern	Not listed	Not listed	y	y
<i>Vulpes vulpes fulva</i>	American red fox	x		Least concern	Not listed	Not listed	n	y
<i>Tamiasciurus hudsonicus</i>	American red squirrel	x	x	Least concern	Not listed	Not listed	y	y
<i>Rattus norvegicus</i> *	Brown rat	x		Least concern	Not listed	Not listed	y	n
<i>Tamias striatus</i>	Eastern chipmunk	x	x	Least concern	Not listed	Not listed	y	y
<i>Canis latrans</i> var.	Eastern coyote	x		Least concern	Not listed	Not listed	y	n
<i>Sciurus carolinensis</i>	Eastern gray squirrel	x	x	Least concern	Not listed	Not listed	y	y
<i>Microtus pennsylvanicus</i>	Eastern meadow vole	x		Least concern	Not listed	Not listed	y	n
<i>Pekania pennanti</i>	Fisher	x		Least concern	Not listed	Not listed	y	y
<i>Marmota monax</i>	Groundhog	x		Least concern	Not listed	Not listed	y	n
<i>Mus musculus</i> *	House mouse	x		Least concern	Not listed	Not listed	y	y
<i>Ondatra zibethicus</i>	Muskrat	x	x	Least concern	Not listed	Not listed	y	n
<i>Erethizon dorsatum</i>	North American porcupine	x		Least concern	Not listed	Not listed	y	y
<i>Procyon lotor</i>	Raccoon	x		Least concern	Not listed	Not listed	y	y
<i>Lontra canadensis</i>	River otter	x		Least concern	Not listed	Not listed	y	y
<i>Odocoileus virginianus</i>	White-tailed deer	x		Least concern	Not listed	Not listed	y	y
Birds								
<i>Corvus brachyrhynchos</i>	American crow	x	x	Least concern	Not listed	Not listed	y	y
<i>Falco sparverius</i>	American kestrel		x	Least concern	Not listed	Not listed	y	n
<i>Turdus migratorius</i>	American robin	x	x	Least concern	Not listed	Not listed	y	y
<i>Chlidonias niger</i>	Back tern		x	Least concern	Not listed	Special concern	y	n
<i>Haliaeetus leucocephalus</i>	Bald eagle		x	Least concern	Not listed	Special concern	y	y
<i>Icterus galbula</i>	Baltimore oriole		x	Least concern	Not listed	Not listed	y	n
<i>Poecile atricapillus</i>	Black-capped chickadee		x	Least concern	Not listed	Not listed	y	y
<i>Cyanocitta cristata</i>	Blue jay		x	Least concern	Not listed	Not listed	y	y
<i>Toxostoma rufum</i>	Brown thrasher		x	Least concern	Not listed	Not listed	y	y
<i>Branta canadensis</i>	Canada goose	x	x	Least concern	Not listed	Not listed	y	y
<i>Bombycilla cedrorum</i>	Cedar waxwing		x	Least concern	Not listed	Not listed	y	n
<i>Spizella passerina</i>	Chipping sparrow	x	x	Least concern	Not listed	Not listed	y	y
<i>Quiscalus quiscula</i>	Common grackle	x	x	Near threatened	Not listed	Not listed	y	y
<i>Gavia immer</i>	Common loon		x	Least concern	Not listed	Not listed	y	y
<i>Mergus merganser</i>	Common merganser		x	Least concern	Not listed	Not listed	y	n

(Continues)

TABLE 1 (Continued)

Species		Assessment method		Status			Detected	
Scientific name	Common name	Camera	Visual	Global	Canada	Ontario	Inside of an EPA	Outside of an FPA
<i>Sterna hirundo</i>	Common tern		x	Least concern	Not listed	Not listed	y	y
<i>Tyrannus tyrannus</i>	Eastern kingbird	x	x	Least concern	Not listed	Not listed	y	y
<i>Aquila chrysaetos</i>	Golden eagle		x	Least concern	Not listed	Endangered	y	n
<i>Ardea herodias</i>	Great blue heron	x	x	Least concern	Not listed	Not listed	y	y
<i>Myiarchus crinitus</i>	Great crested flycatcher	x	x	Least concern	Not listed	Not listed	y	y
<i>Dumetella carolinensis</i>	Grey catbird	x		Least concern	Not listed	Not listed	y	n
<i>Leuconotopicus villosus</i>	Hairy woodpecker		x	Least concern	Not listed	Not listed	y	n
<i>Charadrius vociferus</i>	Killdeer		x	Least concern	Not listed	Not listed	y	n
<i>Anas platyrhynchos</i>	Mallard		x	Least concern	Not listed	Not listed	y	n
<i>Falco columbarius</i>	Merlin		x	Least concern	Not listed	Not listed	n	y
<i>Zenaida macroura</i>	Mourning dove		x	Least concern	Not listed	Not listed	n	y
<i>Cygnus olor</i> *	Mute swan		x	Least concern	Not listed	Not listed	y	n
<i>Cardinalis cardinalis</i>	Northern cardinal		x	Least concern	Not listed	Not listed	y	y
<i>Pandion haliaetus</i>	Osprey		x	Least concern	Not listed	Not listed	y	y
<i>Dryocopus pileatus</i>	Pileated woodpecker		x	Least concern	Not listed	Not listed	n	y
<i>Buteo jamaicensis</i>	Red-tailed hawk		x	Least concern	Not listed	Not listed	y	n
<i>Agelaius phoeniceus</i>	Red-winged blackbird	x	x	Least concern	Not listed	Not listed	y	y
<i>Larus delawarensis</i>	Ring-billed gull		x	Least concern	Not listed	Not listed	y	y
<i>Meleagris gallopavo</i>	Wild turkey	x		Least concern	Not listed	Not listed	n	y
<i>Cathartes aura</i>	Turkey vulture		x	Least concern	Not listed	Not listed	y	y
<i>Hylocichla mustelina</i>	Wood thrush		x	Least concern	Threatened	Special concern	n	y
<i>Setophaga coronata</i>	Yellow-rumped warbler		x	Least concern	Not listed	Not listed	n	y
Frog								
<i>Lithobates catesbeianus</i>	American bullfrog		x	Least concern	Not listed	Not listed	y	y
<i>Lithobates clamitans</i>	Green Frog		x	Least concern	Not listed	Not listed	y	y
<i>Lithobates pipiens</i>	Northern leopard frog		x	Least concern	Not listed	Not listed	y	y
<i>Lithobates sylvaticus</i>	Wood frog		x	Least concern	Not listed	Not listed	y	n
Turtle								
<i>Chrysemys picta</i>	Painted turtle		x	Least concern	Special concern	Not listed	y	y
<i>Graptemys geographica</i>	Northern map turtle		x	Least concern	Special concern	Special concern	y	y
<i>Chelydra serpentina</i>	Snapping turtle	x		Least concern	Special concern	Special concern	y	n

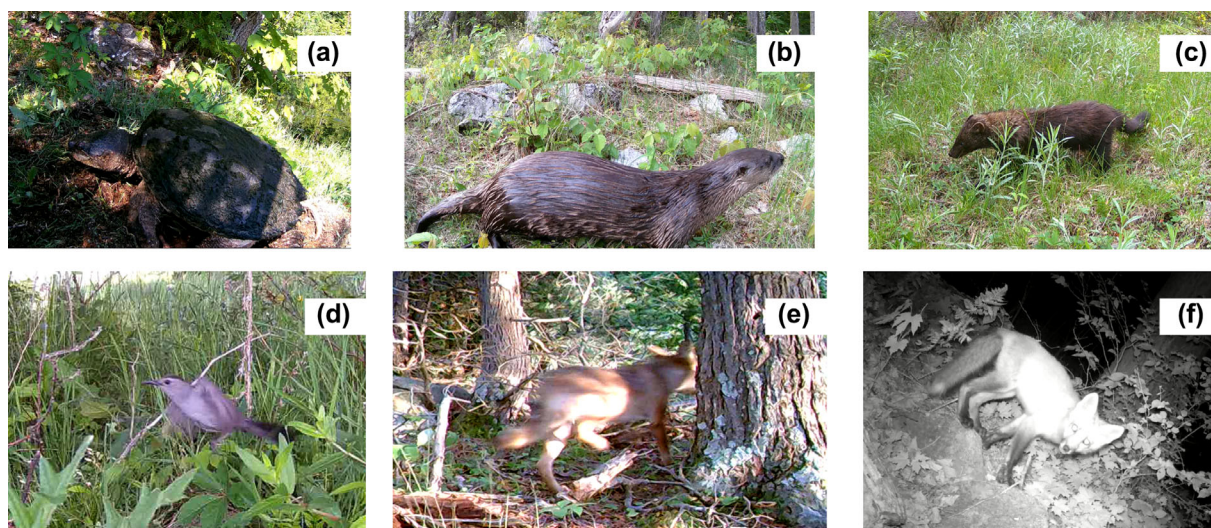
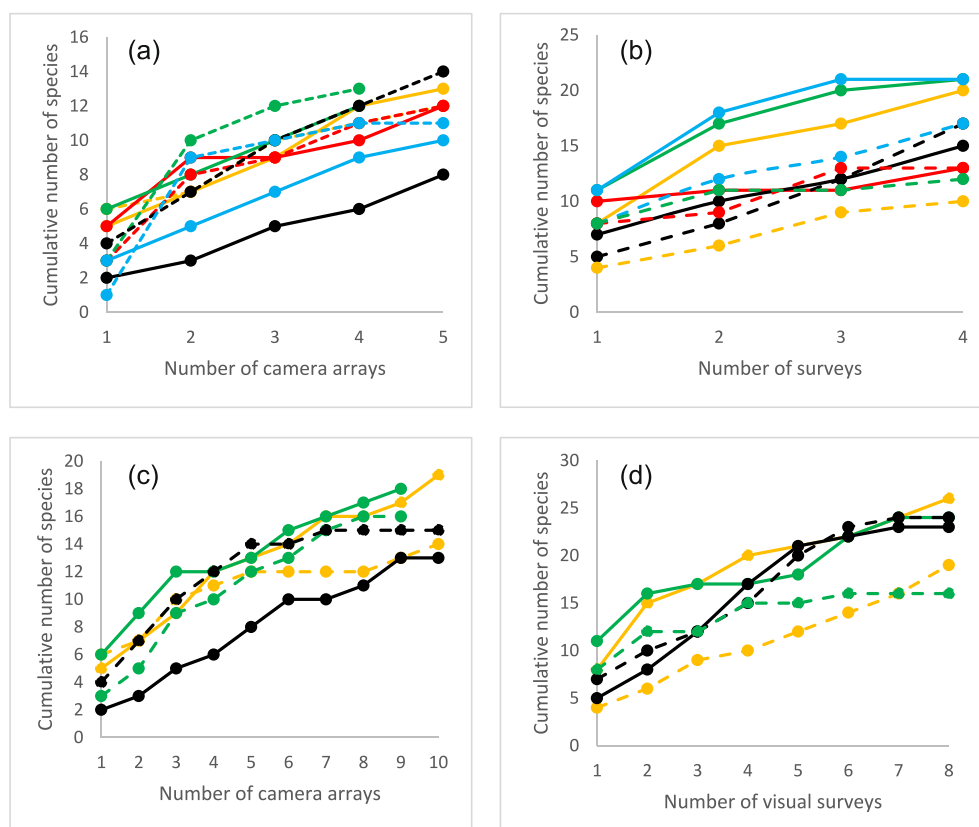


FIGURE 3 Examples of riparian wildlife recorded on cameras: (a) common snapping turtle (*Chelydra serpentina*), (b) North American river otter (*Lontra canadensis*), (c) fisher (*Pekania pennanti*), (d) grey catbird (*Dumetella carolinensis*), (e) Eastern coyote (*Canis latrans* var.) and (f) American red fox (*Vulpes vulpes fulva*).

FIGURE 4 Raw species accumulation curves. Solid lines are locations inside FPAs, dotted lines are outside, with the same colour denoting a temporally matched pair. At the FPA level: (a) camera arrays and (b) visual surveys. Black (Darling's Bay) and blue (Sugarbush Island) is in Lake Opinicon, red (The Bog) and green (Iron Mine with only 4 camera arrays) is in Newboro Lake and yellow is in Big Rideau Lake. At the lake level: (c) camera arrays and (d) visual surveys. Black is Lake Opinicon, yellow is Big Rideau Lake and green is Newboro Lake.



Due to this result, we calculated Shannon diversity indexes by lake instead of by FPAs, as this gave us more confidence that we detected closer to the true number of species. For each lake, diversity was higher inside the FPAs than outside (Big Rideau Lake inside = 1.52, outside = 1.15; Newboro Lake inside = 1.69, outside = 0.96; Lake Opinicon inside = 1.56, outside = 1.14).

4 | DISCUSSION

The two sampling methods employed in our study recorded a diverse range of species including common and rare species that utilized different habitats within and surrounding freshwater protected areas. Freshwater-protected areas had a variable but overall positive

influence on riparian wildlife biodiversity, hosting more bird, mammal, amphibian and reptile species than non-protected areas. Although the protection of additional species was not a focus during their establishment, this result supports the umbrella species hypothesis (Roberge & Angelstam, 2004; Runge et al., 2019) whereby the protection of largemouth bass by banning fishing in these areas led to increased biodiversity of the broader wildlife community.

In general, these lakes have moderately developed shorelines (cottages and docks) and are popular for outdoor recreation, especially boating and fishing. Since all five FPAs are characterized by less human disturbance than non-protected areas, it could be that reduced human disturbance in the FPAs maintained habitat quality and thus resource availability. The presence of human-made structures in the landscape can affect habitat quality and connectivity, influencing species distributions in these areas (Mensing et al., 1998; Robertson & Flood, 1980). Additionally, areas outside of FPAs have more roads (to provide access to cottages), which may impact animal movement (Shanley & Pyare, 2011) and contribute to mortality (Trombulak & Frissell, 2000). In contrast, protected areas were surrounded by mature mixed-wood forest which provides a corridor for wildlife movement and increases accessibility to the shoreline (Hilty & Merenlender, 2004). Furthermore, a study on Big Rideau Lake identified reductions in riparian scavenger diversity and scavenging opportunity with increased proximity to riparian development (Etherington et al., 2023) and in small water bodies, the presence of dogs decreased the diversity of songbirds and fish (Schafft et al., 2024). In contrast, some species may increase in abundance due to the presence of humans. Tolerant small mammals (such as chipmunks and deer mice) increase while intolerant ones (such as shrews and voles) decrease in response to cottage development and the creation of edge habitat (Racey & Euler, 1982). Our results do not align with this, as we found two species of tolerant small mammals (brown rat and Eastern meadow vole) inside but not outside FPAs, and approximately double the number of chipmunks were seen inside compared to outside FPAs. Opportunistic species such as raccoons may also be attracted to artificial food sources such as garbage and may utilize docks or cottages as shelter (Prange et al., 2004), though we found raccoons in both locations. Aside from the impacts of human infrastructure, greater levels of human recreation (e.g., fishing, boating) along shorelines outside the FPAs may lead to avoidance behaviour in some species (Boyle & Samson, 1985). FPAs were largely free of disturbance from boating traffic due to the year-round prohibition of fishing (<https://www.ontario.ca/document/ontario-fishing-regulations-summary/fisheries-management-zone-18>) and few cottages, plus these areas are difficult to navigate (heavily vegetated and shallow); no boat channels were visible during our surveys.

In addition to the direct effects of land conversion on species abundance, there may be indirect effects of having protected areas. The water-land interface is important for abiotic and ecological interactions as the riparian zone stabilizes banks, provides woody material, filters pollutants and regulates water temperature (Acreman et al., 2020; Gallagher et al., 2016; Hoppenreijis et al., 2024; Krause

et al., 2017; Pusey & Arthington, 2003; Richardson et al., 2010). Previous work has found that the abundance and biomass of largemouth bass and shiners is higher in these FPAs (Zolderdo et al., 2019), suggesting foraging opportunities or habitat quality within protected areas may be greater than habitats outside of these areas. This is similar to other studies showing that FPAs with better quality riparian areas had higher diversity of fishes (Sarkar et al., 2013), that riparian habitat quality affected species richness more than recreational fishing (Nikolaus et al., 2021), and that no-access riparian areas resulted in greater fish and songbird abundance (Nikolaus et al., 2022), with intact forests providing better ecosystem services and a higher diversity of aquatic invertebrates than degraded ones (Hanna et al., 2020). Further, higher densities of fish in the FPAs could indirectly influence surrounding riparian habitat. As fish navigate through their landscape they can modify the substrate, altering water-sediment interactions (Collins et al., 2014). Fish also contribute an immense amount of nutrients to the surrounding landscape through excretion and through their decomposition after death (Grimm, 1988; Levi & Tank, 2013; Vanni, 2002), which in turn drive food-web dynamics and the distribution of consumers.

Few species at any level of threat (i.e., Ontario Species at Risk Act, Canadian Species at Risk Act, or IUCN Red List) were detected during our study. Of the seven species listed in at least one jurisdiction, three (golden eagle, black tern and snapping turtle) were only found within FPAs. The single golden eagle observed was perched in the Little Lake sanctuary. Golden eagles are migratory in southern Ontario (COSSARO, 2022) so this individual was presumably using the area to rest and/or eat before continuing to its breeding grounds. The snapping turtle was nesting on the shoreline, and this species is known to avoid residential habitat (Ryan et al., 2014). Black terns were observed feeding around marshy areas and these lakes are within this species' known breeding areas. Their nests are sensitive to being swamped by waves due to boats (<https://www.ontario.ca/page/black-tern>) so this species may particularly benefit from areas with reduced boat traffic. The wood thrush was the only listed species detected outside but not inside an FPA. As this species prefers large forests, it is unclear why the single observation of this species was in a more developed area. The other three listed species—bald eagles, common grackles and Northern map turtles—were found in both locations. A single bald eagle was seen inside and outside a sanctuary on Lake Opinicon, and map turtles were also only seen in that lake. Common grackles were far more common on Big Rideau Lake (36 individuals) than on the other two lakes (five individuals combined). The three non-native species we detected (brown rats, house mice and mute swans) are all naturalized and well-established in the province. Mute swans were only detected in a Newboro Lake FPA; a single rat was seen inside a Lake Opinicon FPA; and house mice were seen in both locations in all three lakes. Lake-specific differences may result from natural differences in species occupancy due to habitat, disturbance or other factors, or temporal differences as lakes were assessed sequentially.

It is well-known among the conservation literature that there can be different sampling biases associated with various forms of

assessment (MacKenzie, 2009). Our assessment method had a clear influence on the species observed. Indeed, of the 61 species observed in our study, only 23% of them were detected using both methods. Notably, of the 17 mammal species detected with cameras, only 5 were seen during visual surveys, while only two out of 35 species of birds were missed during visual surveys. Further, one species of turtle and no frogs were detected on cameras, compared to two turtle and four frog species detected visually. Thus, the method of assessment used should match the objectives of a monitoring program or study, with cameras working better for mammals and visual surveys working better for birds and herpetofauna, with the most complete assessment requiring both methods (Nuñez et al., 2019). Visual surveys may have identified a few mammals due to avoidance behaviour towards boats or reduced activity of some species during the daytime when those surveys were conducted, and bait was used to attract carnivorous scavengers to cameras but visual surveys had no attractants. Small birds were unlikely to trigger the camera in time or be captured sufficiently for identification, and visual surveys included a large area of inclusion plus sound to count birds.

Sites selected for assessment may have had an influence on the species detected (Yoccoz et al., 2001), although we tried to reduce this as much as possible by selecting areas within and outside the FPAs that had superficially similar habitat characteristics. However, these areas had differences that could not be controlled for, particularly stemming from higher human modification outside FPAs. Biotic characteristics of the FPAs (e.g., extremely dense vegetation such as cattails) also made accessing certain habitats challenging, potentially resulting in less representative sampling of wildlife communities. While a previous study found no difference in aquatic vegetation complexity and substrate type within these same FPAs versus outside them (Zolderdo et al., 2019), we note that shoreline habitat complexity seemed to be greater inside the FPAs, with forest, wetland (shallow marshes with dense shoreline vegetation and muddy ground), rock and grassy sections (Figure 2b,e). In contrast, shorelines outside the FPAs were typically rocky and had little aquatic vegetation. Higher complexity of riparian habitat and vegetation has the potential to support larger populations and a wider range of species (Kaufmann et al., 2014; Maisonneuve & Rioux, 2001; Mao et al., 2019; Nikolaus et al., 2021). The original reason for the provincial government to select these specific areas was to protect largemouth bass spawning areas. It appears this had two unintended consequences. One, these areas already contained the most diverse and complex vegetation of the lake, thus protecting numerous fish species by default. Second, with no recreational fishing allowed and with less appealing shorelines (e.g., few sandy beaches or accessible rocks), fewer people decided to develop and build structures and to go boating in these areas, resulting in the unintended consequences of larger areas of intact habitat and fewer disturbances for riparian wildlife. Although the sanctuaries were not designed with the four principles of conservation in mind (comprehensiveness, adequacy, representativeness and efficiency; Linke et al., 2011) nor to reduce development or meet the needs of co-occurring species, and black

bass is not a typical type of umbrella species, we find some support for the hypothesis that even small sanctuaries created simply as no-fishing zones can also support higher riparian biodiversity (similar to Nikolaus et al., 2022).

It should also be noted that some FPAs appeared to have a more positive impact on biodiversity than others, suggesting that candidate protected areas could be chosen to actively support a higher diversity of multiple non-target species. On a larger scale, it is possible that having FPAs in a lake results in lake-wide higher species abundance and diversity. Protected areas can influence nearby habitats through the transfer and export of species and resources to the surrounding area (Di Lorenzo et al., 2016; Hedges et al., 2010), a possibility that remains to be tested for FPAs. We call for future studies to evaluate the specific mechanisms that could lead to differences in wildlife community structures within FPAs and among lakes.

5 | IMPLICATIONS FOR CONSERVATION

These fish sanctuaries were established with the explicit goal of protecting black bass. However, the FPAs may also serve a higher-level benefit, where the reduction in human activity or development results in an umbrella effect for other species (Roberge & Angelstam, 2004; Runge et al., 2019). By reducing disturbances and keeping connectivity between inland, shoreline and aquatic habitats, diverse biological communities and ecological processes can be supported, along with buffering these communities against future pressures. Based on species distribution and shoreline habitat diversity, we recommend that these remaining relatively intact FPAs be afforded additional protection by reducing the potential for anthropogenic alteration. Holistic protection programs focusing on maintaining connectivity to other habitats and riparian diversity are necessary to secure the diverse range of species found in these protected areas (Piczak et al., *In Press*), otherwise we will continue to lose species as thresholds are crossed. Our study raises awareness of the secondary benefits of FPAs, and we advocate for greater study, implementation and monitoring of FPAs as we attempt to overcome the freshwater biodiversity crisis facing the planet (Albert et al., 2021; Harrison et al., 2018).

AUTHOR CONTRIBUTIONS

The project was conceived by Dusevic, Gallagher, Zolderdo and Cooke. Data were collected by Dusevic, Etherington and Lepine. Peiman and Dusevic analysed data and wrote the manuscript with support from all co-authors. Data used in this study was collected for the purpose of this research and can be made available by request.

CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data are available upon request.

ETHICS AND PERMIT APPROVAL STATEMENT

Animal care protocol number 119111, following CCAC guideline number 113 and Cooke Lab SOP #3; also the Ontario Ministry of Natural Resources and Forestry and Parks Canada provided research permits.

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