Impacts of Invasive Species in the Laurentian Great Lakes

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Contents

Abstract The Laurentian Great Lakes are subject to numerous anthropogenic perturbations, among which invasive species are notable. Sequential invasions of non-indigenous species have had profound effects within the basin's ecosystems. Invasive species have altered ecosystem functioning, trophic dynamics, and nutrient

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cycling. They have similarly been implicated in affecting contaminant dynamics, including their transport and bioaccumulation. This work is a regional synthesis of aquatic invasive species-induced changes to ecosystem functioning in the Great Lakes and their tributaries. We have highlighted several species whose impacts on legacy contaminant, nutrient, and food web dynamics in these lakes have been particularly strong. Profiled species included filter feeders [zebra mussels (*Dreissena polymorpha*) and quagga mussels (*D. rostriformis bugensis*)], a fish [round goby (*Neogobius melanostomus*)], and two invasive plants [common reed (*Phragmites australis*) and cattail (*Typha* spp.)]. Collectively, these species showcase invasive species' ecosystem-wide effects. The Great Lakes have a long invasion history. Despite extensive research efforts, complex food web interactions and synergies between invasive species and concomitant stressors can obscure causality. These interactions underscore the need for long-term, spatially resolved studies to understand invasive species' direct and indirect effects on invaded ecosystems.

Keywords Contaminant, Food web, Impact, Invasive species, Laurentian Great Lakes

1 Introduction

The Laurentian Great Lakes provide valuable ecosystem services and harbor the earth's largest freshwater reservoir. The lakes are, however, subject to numerous stressors including toxic chemicals, nutrient loading, and climate change [1], which may interact synergistically [2]. These stressors have caused extensive but often unpredictable changes over the past few decades. Invasive species – non-indigenous species that cause ecological, economic, or health problems – are one of the most important stressors in the Great Lakes [1, 3]. As such, they serve as one of nine high-level indicators of water quality and ecosystem health for the basin [4].

The Great Lakes are a classic example of a mass biological invasion [5]. The system contains the greatest number of non-indigenous species of any studied freshwater system [6] (Fig. 1), whose annual economic impacts exceed $800 million [7]. Commercial shipping during the twentieth century spurred non-indigenous species' introductions [8], whose ballast water has been the dominant transportation vector in recent decades [6]. This invasion rate has increased over the past two centuries owing to greater economic activity (i.e., introduction effort) [9] and, possibly, facilitation between non-indigenous species (an "invasional meltdown") [9, 10].

Studies of invasion have historically focused on terrestrial ecosystems at the expense of the aquatic [11]. However, high invasion rates in freshwater habitats underscore the need to better characterize their effects [6]. Freshwater systems are also extremely sensitive to anthropogenic stressors and harbor a greater proportion

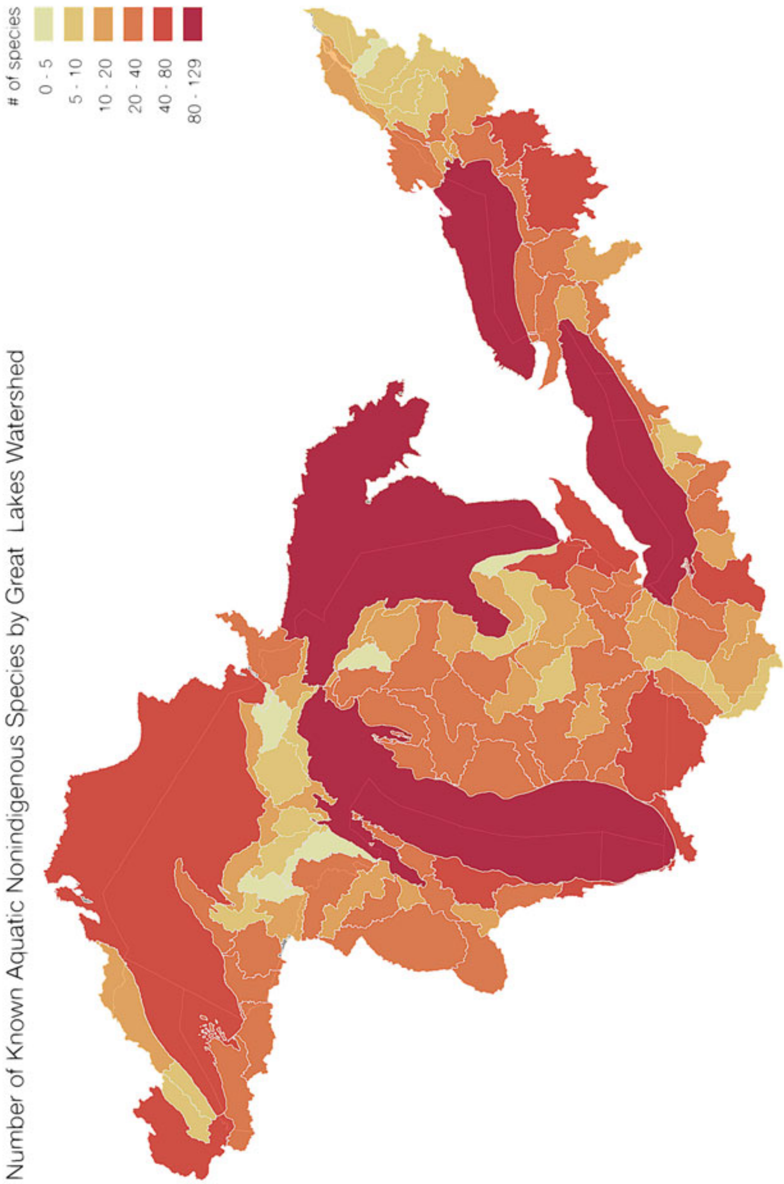

Fig. 1 Distribution of non-indigenous species throughout the Laurentian Great Lakes and their tributaries. Reproduced with permission from NOAA-Great Lakes Aquatic Nonindigenous Species Information System (GLANSIS). https://www.glerl.noaa.gov/glansis/graphics/glansisMap.png

of high-impact invasive species relative to their marine counterparts [11]. Over one-third of non-indigenous species in the Great Lakes have significant ecological or socioeconomic impacts [12, 13], which are cumulatively deteriorating the basin's state [4]. These impacts are appreciably broad. Many invasive species are prey for native predators or predate upon native species. Thus, they have the potential to induce food web shifts [14–16], alter energy pathways [17], and trigger trophic cascades [18]. Lake Erie's food web structure has been most significantly impacted at the hands of anthropogenic activity, in part due to the presence of invasive species [19].

On the heels of regulations to restore their health [20], the Great Lakes have undergone numerous changes [21, 22]. Many such changes were facilitated by reductions in nutrient point loading [21] and anthropogenic mercury (Hg) deposition to the basin [reviewed in 23]. Despite these efforts, the basin is still plagued by a myriad of contaminant-related issues. Nearshore algal blooms persist [4], and contaminant burdens in many fish have either plateaued or increased [15, 23–25]. Indeed, these contaminant levels still often exceed consumption guidelines [4, 26]. Invasive species are implicated in many of these trends [23–25].

Invasive species may occur alongside (i.e., additive) or interact with (i.e., synergistic) other environmental stressors, including nutrient loading and toxic chemicals [1, 2, 11] (Fig. 2). Synergies between invaders may further exacerbate their effects on nutrients and other contaminants in this system [10, 27]. Long-term ecosystem changes, nutrient trends, and contaminant dynamics have been monitored through various government-led programs (reviewed in [22, 28–31]). These and other datasets may be used to examine invasive species' effects on contaminant dynamics in the Great Lakes basin.

The purpose of this chapter is to explore recent findings with respect to invasive species' direct and indirect effects on nutrient and legacy chemical contaminant dynamics in the Great Lakes and their tributaries and to highlight current knowledge gaps. We utilized an indicator species approach, including species such as benthic filter feeders (*Dreissena polymorpha* and *D. rostriformis bugensis*), a benthic fish (*Neogobius melanostomus*), and two invasive wetland plants (*Phragmites australis* and *Typha* spp.). Each of the aforementioned is a model invasive species, having demonstrably affected the structure and function of Great Lakes ecosystems. Furthermore, these species occupy different components of the food web, allowing us to explore implications of their presence on benthic, pelagic, and coastal ecosystems. Collectively, they underscore the breadth of invasive species' impacts on contaminant dynamics and nutrient cycling. In this chapter, we examined effects on stable isotopes, nutrients, and a range of legacy contaminants including polychlorinated biphenyls (PCBs) and heavy metals, highlighting alterations in cycling, availability, magnification, and ratios. We constrained our scope to developments over the past 5 years.

To identify relevant papers published during the period of interest (2014 through November 2019 inclusive), we conducted a systematic literature review using ISI Web of Knowledge and Scopus for the terms: ("invasive species" or "non-native species" or "alien species" or "non-indigenous species" or "exotic species") and

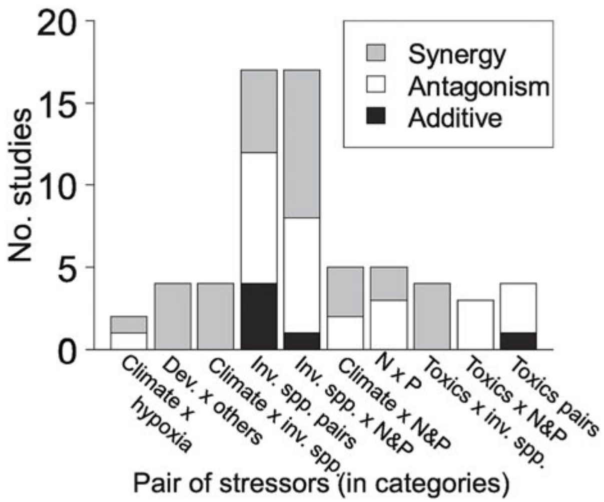

Fig. 2 Interactions between concomitant stressors in the Great Lakes basin and the frequency of their study, separated by interaction type. Interactions have been partitioned into synergies, antagonisms, and additive effects. Interactions between invasive species – and with other stressors – are depicted. *Inv. spp.* invasive species; *N* × *P* nitrogen loading × phosphorus loading, *climate* climate change, *Dev.* coastal urban development. Reprinted from Ecological Indicators, Vol 101, Smith SDP, Bunnell DB, Burton Jr. GA, Ciborowski JJH, Davidson AD, Dickinson CE, Eaton LA, Esselman PC, Evans MA, Kashian DR, Manning NF, McIntyre PB, Nalepa TF, Pérez-Fuentetaja A, Steinman AD, Uzarski DG, Allan JD, Evidence for interactions among environmental stressors in the Laurentian Great Lakes, 203–211, 2019, with permission from Elsevier

("contamina*" or "nutrient" or "environmental chemistry" or "isotope") and ("great lakes"). We restricted our focus to studies on the aforementioned focal species. Using the complement of studies derived from this search, we added additional papers cited therein, as well as recent papers of which we were aware.

2 Dreissenid Mussels (*Dreissena polymorpha* and *D. rostriformis bugensis*)

2.1 Overview

Dovetailing the Great Lakes Water Quality Agreement between Canada and the United States [20], nutrient abatement programs successfully suppressed point loading of phosphorous (P) throughout the Great Lakes, with major declines between 1980 and 2008 [32]. Despite ongoing management efforts, basin-wide nutrient conditions are deteriorating [4, 33], which have in part been attributed to invasive mussels.

The zebra mussel (*Dreissena polymorpha*) and its congener the quagga mussel (*D. rostriformis bugensis*) (hereafter dreissenid mussels) were introduced to the Great Lakes shortly after the binational agreement was ratified. Invasive dreissenids were first detected in Lake Erie – zebra mussels in 1986 [34] and quagga mussels in 1989 [35] – after which both species spread widely. Dreissenids have demonstrably affected the Great Lakes, to the extent that they have been classified as the top environmental stressor [36]. As ecosystem engineers [37], dreissenids have had significant top-down and bottom-up effects throughout the Great Lakes. Below we highlight many of the changes to nutrient, stable isotope, and legacy contaminant dynamics associated with these species.

2.2 Phosphorous

Dreissenid mussels (*Dreissena polymorpha* and *D. rostriformis bugensis*) have affected waterbodies throughout the basin both directly and indirectly. In the former, dreissenids amplify the rate at which particulates are removed from the water column and sequestered into the sediment [38, 39]. In the latter, dreissenids assimilate P in their soft tissues and shells or excrete it as feces or pseudofeces into the sediment-water interphase [40–42]. Excreted P subsequently stimulates primary production in the nearshore benthic region [37, 42].

By tying up available nutrients in the nearshore and impeding offshore availability for primary producers, dreissenids have created “feast and famine” conditions in primary production [4] and an aptly termed “nearshore shunt” [37, 43]. Consequently, dreissenids are concomitantly implicated in eutrophication of the nearshore benthic zone and oligotrophication of the offshore pelagic zone [39–42, 44, 45]. Observed decreases in total P offshore are consistent with bottom-up effects of dreissenids [38, 39, 46] and are concordant with their spread [47]. Ultimately, low P concentrations offshore may impede the basin’s ability to support productivity [4, 46]. Continued nutrient loading from tributaries may further exacerbate this dichotomy [48], highlighting the complex interactions between dreissenids and other anthropogenic stressors.

2.3 Stable Isotopes

Stable isotope analyses can help assess invasive species’ food web changes [49] and have recently been co-opted to quantify long-term effects of dreissenids to aquatic ecosystems. The dreissenid invasion has resulted in the predominance of nearshore energy channels (described above). This has altered trophic dynamics of food webs within the basin, particularly in Lake Michigan [17]. Long-term datasets for lakes Michigan, Huron, Ontario, and Erie have reported dramatic declines in *Diporeia*, an amphipod involved in energy cycling [4, 50, 51]. These declines were coincident with the dreissenid invasion and spread [4, 14, 50, 51] which may have inhibited *Diporeia* foraging [52]. Through reduced prey availability, dreissenids appear to have forced dietary shifts in top predatory species, increasing the reliance of pelagic fish on nearshore benthic energy channels [14, 17]. This has corresponded to δ13C enrichment and δ15N declines in the pelagic and profundal fish community relative to baseline [17]. Similar benthic energetic shifts have been reported elsewhere for Lake Michigan [53] and Lake Ontario [54]. These phenomena underscore the extent to which these mussels have contributed to restructuring food webs basin-wide.

2.4 Carbon, Nitrate, and Silica

Dreissenids have caused extensive basin-wide changes to carbon (C) dynamics and biogeochemical cycling [55]. In particular, lakes Michigan, Huron, Erie, and Ontario have undergone carbon dioxide (CO_2) supersaturation, with the most demonstrable changes occurring in Lake Michigan's heavily infested waters [55]. Observed increases in the partial pressure of CO_2 (pCO_2) have also been attributed to the dreissenid invasion [55].

In addition to the above-described impacts, decreases in particulate C in both Lake Michigan and Lake Huron [38, 41], increases in dissolved inorganic C in Lake Ontario [56], and increases in nitrate (NO_3) and silica throughout the basin [38, 41] have similarly been reported. These changes have likewise been ascribed to dreissenids and are concurrent with their spread [38, 41, 57]. Dreissenids have similarly produced ecosystem-wide effects on nutrient dynamics in smaller, inland lakes [42], though these effects appear to be highly context-dependent. In offshore waters of lakes Michigan and Huron, dreissenids' indirect effects predominate over those attributed to direct grazing [41]. In Saginaw Bay, Lake Huron nutrient loading appears to have a stronger influence on the food web than do dreissenids [58]. Green Bay, Lake Michigan, also varies from typical patterns, as the response to the dreissenid invasion is seemingly overwhelmed by nutrient inputs [59].

2.5 Legacy Contaminants

Dreissenids are sentinel organisms for chemical contaminants and bioaccumulative pollutants owing to their prolific filter feeding [60]. Dreissenids mobilize and biomagnify sediment contaminants, whose filtration increases sedimentation of contaminants like titanium dioxide [61] and PCBs [62]. They may thus provide an entry point to benthic food webs [62] once ingested by sediment-dwelling amphipods and chironomids [15].

Dreissenids may act as a conduit for Hg bioaccumulation and accelerate its methylation [63]. Dreissenid-induced shifts in energy pathways have stimulated the proliferation of filamentous benthic green algae (*Cladophora glomerata*), whose growth is facilitated by dreissenid pseudofeces [64]. In Lake Michigan, the nearshore benthic zone supports dense dreissenid-*Cladophora* assemblages in which heightened levels of methylmercury (MeHg) are found [63]. Decaying mats of *Cladophora* support MeHg production [65, 66] and facilitate its entry into food webs [63]. Nearshore dreissenids that cohabit with and consume *Cladophora* harbor greater MeHg concentrations relative to offshore mussels [63]. In this way, dreissenids may act as a vector for MeHg bioaccumulation once consumed by top predators, which now disproportionally feed on prey in nearshore benthic regions [17]. By hindering offshore productivity and initiating declines in *Diporeia* populations, dreissenids may also contribute to truncated growth rates and higher Hg loads of top predatory fishes throughout the basin [14, 27, 53].

3 Round Goby (*Neogobius melanostomus*)

3.1 Overview

Non-indigenous fishes can have significant consequences to food web dynamics [67]. The invasive round goby (*Neogobius melanostomus*) is a striking example. The fish was first documented in the St. Clair River in 1990 [68]. By 1999, the species was well-established throughout the Great Lakes [69], whose proliferation appears to have been facilitated by zebra mussels introduced several years prior [70]. As the most abundant non-indigenous vertebrate in the Laurentian Great Lakes-St. Lawrence River basin [71], they have drawn concern over their long-term effects on ecosystem functioning [72]. Below we present an overview of their effects on stable isotopes and legacy contaminants.

3.2 Stable Isotopes

Top predatory fish within the basin have flexibly responded to recent changes in prey availability. In the Great Lakes, round goby (*Neogobius melanostomus*) are heavily predated by piscivores, including brown trout (*Salmo trutta*) [73, 74], smallmouth bass (*Micropterus dolomieu*) [16], steelhead (*Oncorhynchus mykiss*) [75], burbot (*Lota lota*) [76], and lake trout (*Salvelinus namaycush*) [27, 73, 77]. Consequently, foraging patterns of top pelagic predators have shifted to exploit this abundant prey source. Diets of many fishes now include significant contributions from nearshore carbon energy sources in lakes Superior, Huron, and Ontario [27, 74, 77]. Given these dietary shifts, many predatory fishes have lower δ15N and higher δ13C values relative to pre-invasion scenarios [73]. Round goby (*Neogobius melanostomus*) has similarly become the dominant prey item for native benthic lake sturgeon (*Acipenser fulvescens*) in Lake Ontario. δ15N enrichment in sturgeon has been linked to the round goby introduction [78].

3.3 Legacy Contaminants

Synchronized invasions of dreissenids and round goby (*Neogobius melanostomus*) have generated otherwise absent connections between benthic and pelagic food webs in the Great Lakes [79]. Round goby (*Neogobius melanostomus*) serves as a conduit for contaminant uptake and transfer via dreissenid consumption [73], the latter of which act as sentinels for contaminants (as described above). Together, these species have mobilized sequestered pollutants [62, 79] and precipitated changes in contaminant bioaccumulation in upper trophic levels [80]. More specifically, these species have engendered community-wide shifts in contaminant transfer toward the nearshore benthos [17, 27]. This shift has significant implications for fish contaminant burdens. In Lake Erie, round goby (*Neogobius melanostomus*) is the prominent prey for smallmouth bass [16]. This reliance is purported to drive increases in smallmouth bass polybrominated diphenyl ether (PBDE) levels in future years [79].

3.3.1 Hg

Round goby (*Neogobius melanostomus*) is a strong vector for persistent contaminants such as Hg. Round goby (*Neogobius melanostomus*) and dreissenid mussels (*Dreissena polymorpha* and *D. rostriformis bugensis*) have collectively been associated with recent trend reversals in fish Hg concentrations within the basin [81]. For instance, total Hg concentrations in Lake Ontario walleye have remained constant over the past 40 years despite reduced contaminant emissions, due in part to food chain lengthening by invasive species [26]. Round goby (*Neogobius melanostomus*) has also been linked to elevated Hg levels in fish in lakes Huron [27], Michigan [53], and Erie [25]. Namely, the goby and dreissenid invasions into Lake Huron coincided with the collapse of prey populations [82, 83]. Top predatory fish subsequently relied on alternative sources of food – including gobies [27] – which contain lower energy density relative to their preferred prey [84]. This trend is particularly salient in lake trout, whose stunted growth rates and higher Hg concentrations have been linked to the round goby (*Neogobius melanostomus*) invasion across multiple lakes [4, 27, 53]. In Lake Michigan, increased lake trout Hg concentrations were reported following the round goby (*Neogobius melanostomus*) and dreissenid invasions [53]. These changes to Hg bioaccumulation manifested in light of decreased emissions over the period surveyed [85, 86]. In turn, these data indicate the disproportionally negative effect of invasive species on lake trout contaminant burdens [53].

4 Common Reed (*Phragmites australis*) and Cattail (*Typha* spp.)

4.1 Overview

Great Lakes coastal wetlands provide essential ecosystem services [87], filtering nutrient-rich runoff prior to entering larger waterbodies [88]. They also serve as C sinks [89] given their high rates of primary production and slow decomposition [90]. These traits make wetlands highly susceptible to plant invasions [91] which are often aided by sediment and nutrient enrichment [4]. In recent years, Great Lakes wetlands have been subject to elevated nitrogen (N) inputs [92]. This has driven C accretion [93] and facilitated plant invasions [94–96]. Invasive plants are ubiquitous in Great Lakes coastal wetlands, dominating up to 70% of total vegetation cover [97]. The cattail (*Typha* spp.) and common reed (*Phragmites australis*, hereafter *Phragmites*) are presently two of the most successful invasive plants in North American wetlands [91].

Three cattail species are found in the Great Lakes: *Typha latifolia*, the European narrow leaf *Typha angustifolia*, and *Typha* × *glauca*, wherein the latter two species are invasive [98–100]. *Typha x glauca* is a hybrid between native *T. latifolia* and introduced *T. angustifolia* [98] (hereafter, both invasive cattail species will collectively be referred to as invasive *Typha*). Invasive *Typha* is abundant throughout the Great Lakes [101]. Actively displacing native wetland communities, it comprises up to 50% of wetland area in Lake Ontario alone and dominates 13.5% total Great Lakes wetland area [97]. *Typha* has significant and well-documented negative effects on native plant diversity [95, 102], impacts that correlate positively with its stand age [102]. Highly dense *Typha* stands produce prodigious amounts of litter, which accumulate for decades following its invasion [103]. Among other effects, its high litter mass may imperil fish community diversity by stimulating anoxic conditions. In a Lake Michigan coastal wetland, *Typha*'s recalcitrant litter led to reductions in fish abundance and diversity by reducing dissolved oxygen levels [104]. *Typha*'s presence may also facilitate the establishment of other aquatic invasive plants [105], further extending the span of observed impacts.

Phragmites is one of the worst invasive species in North American wetlands [106], of which two strains are present in North America [107]. The invasive Eurasian strain is now ubiquitous throughout the Great Lakes [108] where it is particularly abundant in Lake St. Clair, Lake Huron, and Lake Michigan [4]. While the lower Great Lakes are at most immediate risk for further expansion, climate change will likely also increase susceptibility of the upper Great Lakes' coastal zones [109]. *Phragmites* is adept at colonizing nutrient-rich systems, effects of which are extensive. *Phragmites* negatively influences plant biodiversity [95] and threatens 25% of at-risk species in Ontario alone [110].

Relative to native species, *Phragmites* and *Typha* have greater aboveground biomass [96, 111, 112] and produce larger amounts of recalcitrant litter [95, 111]. They also have tremendous capacities for nutrient removal. Indeed, their larger relative sizes may permit access to more resources and portend a competitive advantage relative to comparative natives [94, 113]. Below, we summarize their effects on N and C dynamics and their interactive effects with other anthropogenic stressors.

4.2 Nitrogen

Both invaders alter nutrient cycling regimes [94, 102], promoting greater N retention relative to native species [94, 112]. *Typha* increases inorganic N soil pools [103, 114]. Sites invaded by *Typha* often exhibit higher soil organic matter, NO_3, and ammonium (NH_4^+) concentrations relative to native sites, as demonstrated in coastal wetlands abutting lakes Michigan and Huron [102, 114, 115]. Wetlands dominated by *Typha* also boast higher denitrification potentials relative to those dominated by native species [102]. These effects correlate positively with stand age [102]. Despite the ecosystem services *Typha* confers, benefits must be gauged against their strong negative effects and measured over time [102]. Indeed, *Typha*'s positive ecosystem functions were temporally mediated in a Lake Michigan wetland [115]. Similar trade-offs between ecosystem services are likewise apparent for *Phragmites* [112].

Litter decomposition rates of common reed (*Phragmites australis*) and cattail (*Typha* spp.) are similar [116]. In two inland Michiganian lakes, the invasions of both plants increased organic matter storage and aboveground biomass N stocks [95]. While *Phragmites'* leaves have a higher N content relative to *Typha*, both plants had similar effects on N standing stocks in a Lake Erie coastal marsh [112]. *Typha*'s slow-decomposing plant litter also appears to be disproportionately responsible for its impacts on ecosystem functioning [114]. Their litter increases inorganic N and N mineralization rates and has been implicated in the decline of native plant richness and abundance [114].

Interestingly, [117] found no difference in NO_3, ammonia (NH_3), soil organic matter, or denitrification potentials between inland Lake Michigan wetland areas dominated by invasive *Phragmites* relative its native counterpart. Despite these similarities, *Phragmites* growth in Lake Michigan wetlands was more positively correlated with nutrient availability – in particular, inorganic N [118] – a testament to its efficient resource use.

Both invaders are adapted to nutrient-rich habitats and interact synergistically with nutrient loading [4, 109, 119]. Ecosystem modelling suggests that nutrient loading fuels *Typha* dominance [119] and *Phragmites* presence [109]. However, nutrient effects on *Phragmites* distribution may be lake and context-specific [109, 118]. Notwithstanding potential context dependencies, this synergy suggests that a more nuanced management strategy – reduced external nutrient loading – may provide an attractive alternative to traditional herbicide management [119].

4.3 Carbon

The dominance of both invaders is positively related to aboveground biomass and C standing stocks [95, 112]. Common reed (*Phragmites australis*) and cattail (*Typha* spp.) promote C accumulation in surface litter and soils [102, 111, 112, 116], even under low N levels [93]. In doing so, these invaders have the capacity to significantly alter the structure and function of coastal wetlands [93].

Together, these plants drive wetland C accretion through increased primary productivity [93]. *Phragmites* can affect C cycling through high rates of C assimilation [120] and net primary production [116]. These rates often exceed those of native meadow marsh [112]. Stemming from their greater maximum size, wetlands invaded by *Phragmites* may promote greater C storage relative to *Typha* [93]. *Phragmites* may also disproportionately alter wetland C budgets, whose sediment CO_2 release is greater than in *Typha* sediments [116]. Conversely, *Typha* monospecific stands have greater C mineralization rates and more labile soil organic matter relative to *Phragmites* [95]. Despite these disparities, effects on annual C stocks appear to be similar [112]. While *Phragmites* promoted greater C assimilation relative to native meadow marsh in a Lake Erie coastal marsh, assimilation rates and C stocks were equal to that of *Typha* [112].

Typha soil methane (CH_4) emissions are thrice that of native-dominated mesocosms, due in part to their greater aboveground biomass and productivity [111]. These emission rates also exceed that of *Phragmites,* which may reduce CH_4 emissions from sediments [116]. Importantly, nutrient loading may indirectly facilitate greater CH_4 emissions by stimulating *Typha* productivity [111], exacerbating the already high global warming potential of wetlands [121].

5 Knowledge Gaps

In this chapter, we summarized recent research on several invasive species' effects on legacy contaminant, chemical, and nutrient dynamics in the Great Lakes basin. Disentangling invasive species' effects from the milieu of stressors with which they co-occur continues to be problematic. Several factors complicate cause-and-effect relationships. Other current and sometimes-synergistic anthropogenic stressors – such as nutrient loading – may obfuscate invasive species' relative effects [52, 93]. Modelling may offer one way to unravel ecosystem-level effects of invaders [52], and their application is encouraged.

Invasive species represent an unprecedented energy pathway. However, their influences on contaminant bioaccumulation and biomagnification require further study [27, 79]. Broad effects are difficult to infer given that contaminant trends are often system- and species-specific [122] and affected by among-year variability in fish contaminant loads [26]. Indeed, Hg concentrations may exhibit considerable spatiotemporal variation, both within and among trophic levels [24]. Concomitant stressors are also likely to influence legacy contaminant uptake and accumulation [24, 25]. To further complicate matters, the extent to which natives predate upon invasive species is context-dependent in smaller inland lakes [123]. These complexities may ultimately hinder causal inferences.

There is a pressing need for long-term, high-frequency, high-quality data to clarify the mechanisms of invasive species' impacts on nutrient and contaminant dynamics within the Great Lakes. Given high among-lake variability in contaminant patterns [24, 124], responses to invasive species are likely to vary between systems and spatially and temporally within a system [2, 51]. Differences in temporal resolution [38] and high inter-annual variation in time series data [52] can also obstruct clear trends by providing competing results. These context dependencies are similarly applicable in coastal wetlands [112], wherein impacts of invasive plants often only materialize over time [102]. Such system contingencies can have profound influences on the accurate quantification of invasive species' impacts. These context dependencies emphasize the importance of multi-lake, spatially resolved studies. However, this objective is complicated by the need for binational interagency laboratory cooperation. A coordinated binational strategy is imperative to effectively understand and manage invasive species' impacts throughout the basin. Unfortunately, binational regulations for the management of aquatic invasive species are currently lacking [125].

Data gaps compromise our ability to accurately estimate invasive species' effects on food web dynamics for even the most well-studied lakes [52]. For instance, invasive species' trophic roles are understudied in Lake Michigan, despite being a relatively data-rich waterbody [73]. Furthermore, the paucity of historical baseline diet information for nearshore native predators in Lake Michigan may impede understanding of invasive species' effects on ecosystem processes [73]. In Lake Erie, nutrient dynamics and phosphorous recycling also demand further study [19].

Our review revealed unequally distributed research efforts among our focal species. The recent literature is replete with studies on dreissenid mussels (*Dreissena polymorpha* and *D. rostriformis bugensis*), seemingly at the expense of other invaders. Despite their pivotal role in restructuring ecosystems, such biases may impede a holistic understanding of invasive species' impacts throughout the basin. Research foci within each indicator species also appeared skewed. Round goby (*Neogobius melanostomus*) and dreissenids have collectively shifted food web dynamics, whose impacts are inextricably linked [27, 70, 73, 79, 80]. While frequently reported in unison, future researchers should continue to unravel these species' relative and cumulative influences. Despite being the subject of considerable research, dreissenids' effects on C dynamics are largely unknown (but see [126]). Likewise, the way in which invasive plants influence C accretion – alone and through synergistic interactions with nutrient loading – is unclear [93]. The extent to which *Typha* and *Phragmites* affect nutrient cycling beyond N and C is also ill defined [112]. Collectively, these information gaps have cascading consequences for understanding broad implications of these species' invasions.

6 Conclusion

The Great Lakes have experienced extensive invasive species-induced perturbations in their structure and function. Significant progress has been made over the past several years to understand the extent of these effects. Nevertheless, our review revealed several knowledge gaps, which may impede a comprehensive understanding of invasive species' impacts within the basin. Species' invasions require broad, coordinated approaches in their study and management. Despite recent developments, concerted efforts are essential to further unpack invasive species' ecosystem-level effects on legacy contaminant, nutrient, and food web dynamics.

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