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Functional traits reveal the dominant drivers of long-term community change across a North American Great Lake

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Abstract

Ecosystems worldwide have been impacted by multiple anthropogenic stressors, yet efforts to understand and manage these impacts have been hindered by difficulties in disentangling relative stressor effects. Theoretically, the actions of individual stressors can be delineated based on associated changes in functional traits and these relationships should be generalizable across communities comprised of different species. Thus, combining trait perspectives with community composition data could help to identify the relative influence of different stressors. We evaluated the utility of this combined approach by quantifying shifts in fish species and trait composition in Lake Erie during the past 50 years (1969–2018) in relation to human-driven changes in nutrient inputs, climate warming, and biological invasions. Species and trait shifts were also compared between two Lake Erie basins, which differ in their environmental and biological characteristics, to identify trait responses that were generalizable across different ecosystems versus those that were context dependent. Our analyses revealed consistent species changes across basins, and shifts in feeding and thermal traits, that were primarily associated with altered nutrient inputs (oligotrophication followed by eutrophication). We found no or inconsistent trait-based evidence for the effects of warming and two invasive fishes. Context-dependent trait responses were also evident; nutrient inputs were related to shifts in species tolerant of turbidity in the shallow, eutrophic western basin, which contrasted to shifts between benthopelagic and benthic species in the deeper central basin. Our results reveal the dominant effects of specific stressors on a large freshwater lake and offer a framework for combining species-based and trait-based approaches to delineate the impacts of simultaneous stressors on communities of perturbed natural ecosystems.

KEYWORDS
anthropogenic, climate change, community composition, eutrophication, functional traits, invasive species, multiple stressors, temporal

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1 | INTRODUCTION

The world's ecosystems are being threatened by an array of anthropogenic stressors, including climate change, eutrophication, biological invasions, and over-exploitation (Ellis, 2011; Halpern et al., 2015; Ormerod et al., 2010). These stressors also commonly co-occur, presenting a major challenge for researchers and managers who must disentangle the effects of multiple stressors to understand past dynamics, predict future change, and mitigate impacts (Côté et al., 2016; Downes, 2010). While controlled experiments offer one approach to overcome this challenge (e.g., Darling & Côté, 2008; Jackson et al., 2016), experimental findings are often limited in scope and may not apply across different, natural ecosystems (Orr et al., 2020; Townsend et al., 2008; Yuan, 2010). In such cases, observational approaches that relate stressors to community changes through space or time can incorporate the ecological complexity that experiments often lack. However, collinearity between stressors frequently precludes partitioning their combined effects into individual components (Downes, 2010). These deficiencies point to the need for new approaches that can separate the effects of co-occurring stressors while remaining generalizable enough to identify the dominant drivers across different ecosystems.

A possible solution for disentangling multiple stressor effects across different ecosystems is to incorporate functional traits into traditional species-based analyses (Baattrup-Pedersen et al., 2016; Beukhof et al., 2019; Lange et al., 2014; Statzner & Bêche, 2010). Functional traits can help to link community changes to the actions of individual stressors because each stressor is expected to select or "filter" for species with traits that are well-suited to the new environment and select against (filter out) species with maladapted traits (Verberk et al., 2013). Thus, the actions of individual stressors can theoretically be delineated based on changes in associated traits (Statzner & Bêche, 2010). For example, two correlated stressors might select for species with different traits, such as climate warming selecting for species with higher thermal optima (Diamond et al., 2012) versus an invasive predator selecting for prey with effective antipredator defenses (Sih et al., 2010). A shift in species composition (Figure 1a) that is accompanied by a shift in traits related to both warming and predator defense (Figure 1b) would thus provide evidence that both stressors are responsible for driving community change. Circumstances in which community trait changes do not match the predicted effects of each stressor can help to separate the effects of co-occurring stressors or generate hypotheses about alternative drivers (Figure 1c–e). Despite the potential value of using functional traits to better tease apart multiple stressor effects, such studies are still uncommon compared to species-based research (Baattrup-Pedersen et al., 2016; McLean et al., 2018), highlighting the need for more rigorous testing of this approach.

Although combining species-based and trait-based approaches offers a promising step forward to better understand multiple stressor effects, some limitations exist that also require further research to resolve. Trait approaches have been hypothesized to be more generalizable, in contrast to species-based analyses, because traits can be compared across communities regardless of differences in species composition (Baattrup-Pedersen et al., 2016; McGill et al., 2006). However, whether this concept applies to using traits to delineate stressor effects across different ecosystems remains an open question. As with species, traits are also filtered by the unique local environment associated with each community (Cadotte & Tucker, 2017). The same stressor could therefore filter for different traits in different communities depending upon variability in stressor intensity (Statzner & Bêche, 2010) and how the stressor interacts with local abiotic conditions or biological structure (Gravel et al., 2016; Suding et al., 2008; Verberk et al., 2013). Thus, a trait filtered by a stressor in one ecosystem may not be similarly filtered in another. This uncertainty highlights the need to compare shared versus context-dependent trait responses to the same stressors across different communities.

Additionally, using traits to identify the actions of individual stressors is best accomplished when a unique trait (or set of traits) is selected for or against by each stressor. Unfortunately, knowing in advance whether such relationships exist is difficult because trait datasets and associated analyses are often lacking (e.g., Hamilton et al., 2020). Furthermore, many commonly quantified traits, such as those based on morphology or life history (Cano-Barbacil et al., 2020), can be similarly influenced by more than one stressor. For instance, community body size has been reported to decline in response to a variety of stressors, including warming (Forster et al., 2012) and human exploitation (Palkovacs et al., 2018). A stressor could also propagate unexpected changes in multiple traits if they are genetically linked (e.g., pleiotropy) or co-regulated through historic, evolutionary constraints (Hamilton et al., 2020; Poff et al., 2006; Verberk et al., 2013). Identifying informative traits therefore requires research that evaluates expected associations among stressors and a variety of candidate traits, and that assesses synchronous and thus potentially linked changes in multiple traits.

1.1 | Objectives

We designed a study to address the three knowledge gaps outlined above by (1) comparing species versus trait changes in relation to multiple anthropogenic stressors to evaluate the insights provided by adopting a trait perspective; (2) comparing stressor-related compositional changes across different ecological contexts to identify which trait responses were generalizable versus context dependent; and (3) comparing predicted trait–stressor relationships to observed changes in a variety of candidate traits. Observed trait shifts that matched our predictions provided evidence that compositional changes were driven by the stressor in question and indicate informative trait–stressor relationships (i.e., Figure 1b). By contrast, trait changes that did not match our predictions were used to eliminate spurious relationships (Figure 1c,d) or identify alternate mechanisms such as potential linkages between traits (Figure 1e).
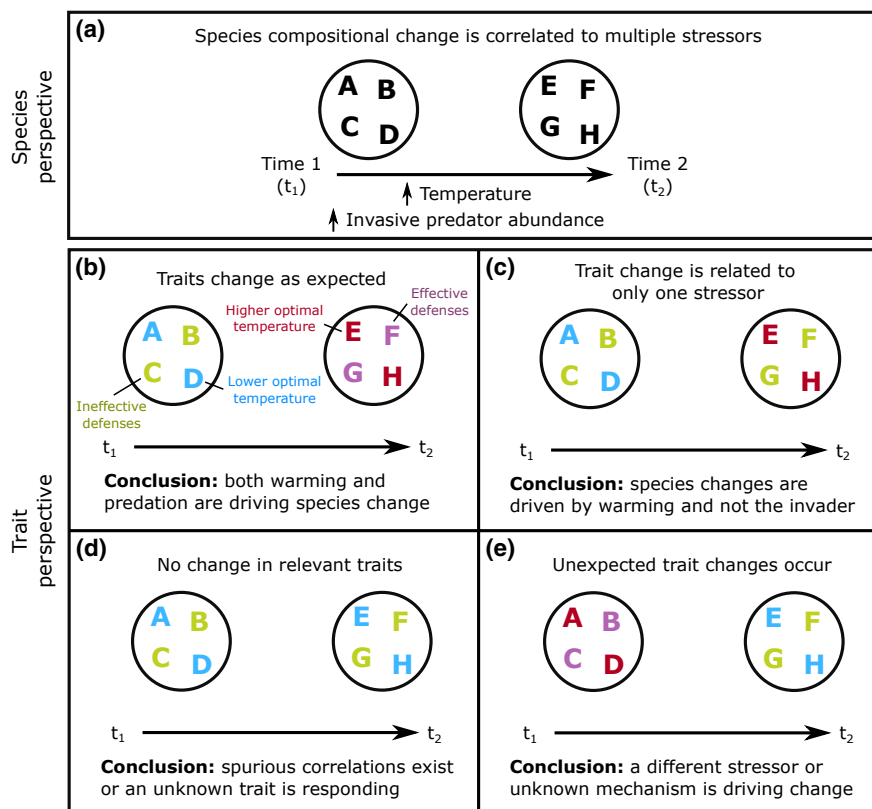
FIGURE 1 Hypothetical examples of how species-based conclusions of the effects of multiple stressors (increasing temperature and an invasive predator) on a community through time (from t_1 to t_2) could be improved by trait-based approaches. In (a), species composition changes (illustrated as letter changes) are correlated with increased warming and predator abundance, and (b) associated trait changes (illustrated as color changes) support this link. In (c), species changes are correlated to both warming and invasion, but associated trait changes suggest warming as the predominant stressor. In (d), no shifts in trait composition occur, suggesting spurious correlations between stressors and species shifts or a response in an unknown trait. In (e), traits change but not as expected, such as species with a low optimal temperature for growth increasing with warming. Such unanticipated trait shifts would suggest that an unmeasured stressor, or alternate mechanism, is driving species shifts

1.2 | Study ecosystem

To achieve our first two objectives, we related long-term (1969–2018) data on anthropogenic stressors in the Lake Erie watershed (USA–Canada) to changes in fish species and trait composition in western and central Lake Erie during the same 50-year period. These two lake basins offer an ideal study system because both have a long history of exposure to common global stressors, including altered nutrient inputs (both eutrophication and oligotrophication), climate warming, and biological invasions (Figure 2; Ludsin et al., 2001; Makarewicz & Bertram, 1991; Scavia et al., 2014). Additionally, both basins support different fish communities because of their unique habitat characteristics (Ludsin et al., 2001), with water temperature and the productivity of the lower food web decreasing, and water transparency and mean basin depth increasing, from the western to central basin (Bunnell et al., 2014; Ludsin et al., 2001; Sly, 1976). This shared history of stressor exposure in basins that differ in their biotic and abiotic characteristics allowed for a comparison of species versus trait changes in different ecological contexts, and for the identification of generalizable versus context-dependent trait responses.

1.3 | Predictions

To achieve our third objective, we used a framework that compared predicted trait responses to different stressors to observed changes in traits related to habitat use, feeding preferences, reproductive life history, physiology, and body size in western and central Lake Erie. These predictions were informed by previous research on the effects of nutrient inputs, climate warming, and invasive species (detailed below and summarized in Figure 3).

Altered nutrient inputs—In Lake Erie, excessive nutrient inputs (i.e., eutrophication) can increase basal resources, such as phytoplankton and benthic algae (Scavia et al., 2014; Watson et al., 2016), which can reduce water transparency in the western basin (Makarewicz & Bertram, 1991; Watson et al., 2016) and exacerbate bottom hypoxia in the central basin (Scavia et al., 2014). Therefore, if nutrients are responsible for driving observed community changes, nutrient-related shifts in composition should also coincide with shifts in the relative prevalence of intermediate consumers (e.g., detritivores and omnivores) that can exploit basal resources versus carnivores (e.g., piscivores and invertivores) that cannot (Figure 3a).
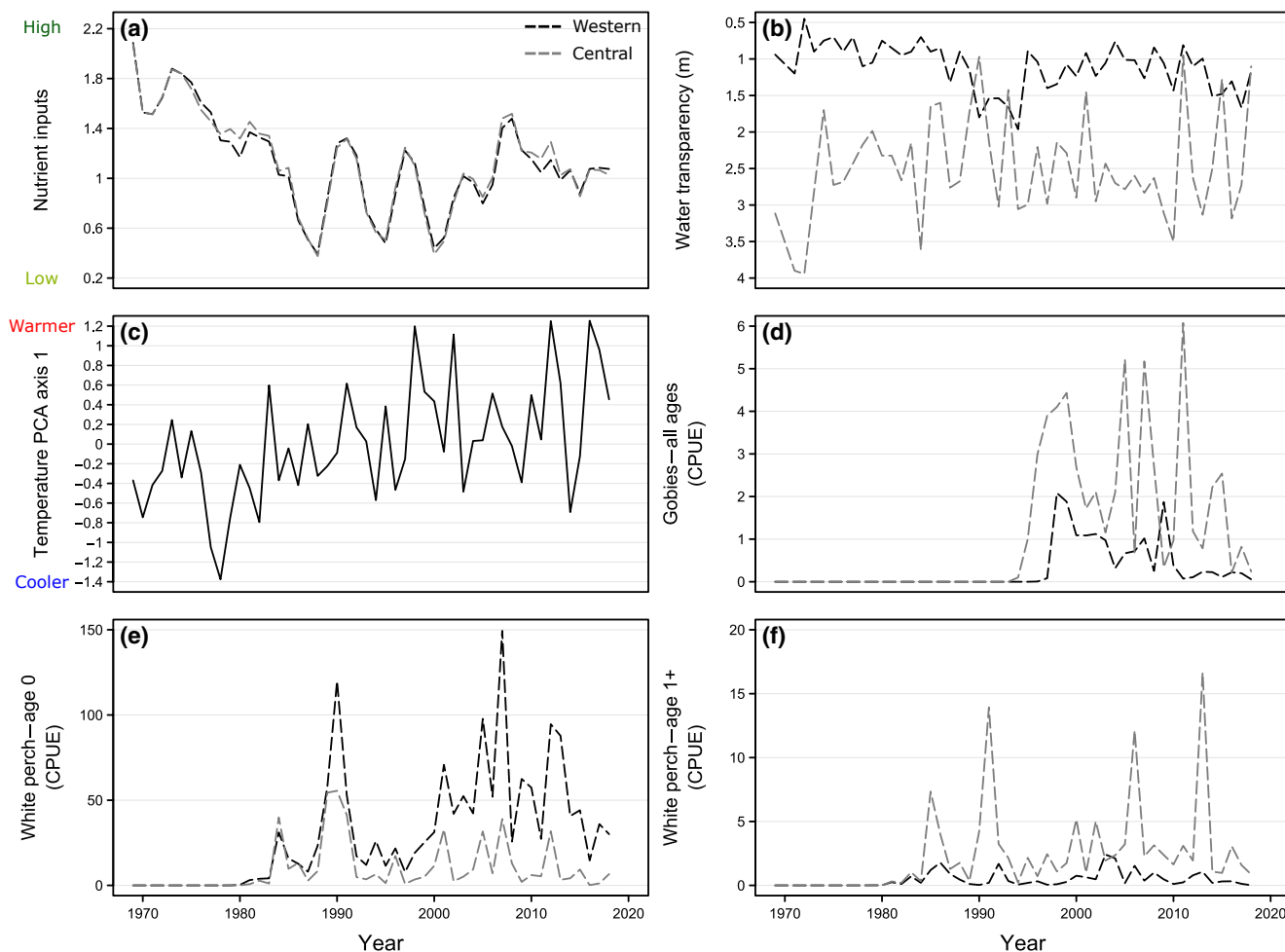
FIGURE 2 Temporal changes in (a) nutrient inputs, (b) water transparency (measured as Secchi depth), (c) temperature, (d) gobies catch-per-unit-effort (CPUE; individuals•trawl min^{-1} of all ages), and (e, f) white perch (CPUE; age-0 and age-1+) in the Lake Erie ecosystem during 1969–2018. Solid lines indicate lakewide estimates for which no basin-specific data exists. Black, dashed lines illustrate data specific to Lake Erie's western basin and grey, dashed lines illustrate data specific to the central basin

Additionally, increased nutrients should benefit species that can tolerate poor water quality (i.e., high turbidity and low oxygen) in the western basin (Ludsin et al., 2001) and benthopelagic species in the central basin that can feed and grow above the hypoxic bottom layer without penalty (Stone et al., 2020).

Climate warming—Increased lake temperatures from climate warming are expected to reduce available habitat for colder-water fishes in both basins (Lynch et al., 2010) and exacerbate hypolimnetic hypoxia in the central basin (Rucinski et al., 2010; Watson et al., 2016). Warming-related shifts in composition should therefore coincide with increased prevalence of warmer-water species that have a higher optimal temperature for growth in both basins, and an increase in benthopelagic species in the central basin owing to bottom hypoxia (Ludsin et al., 2001; Stone et al., 2020; Figure 3b).

Biological invasions—A variety of species have invaded Lake Erie (Munawar et al., 2005), and of these we focused on two invasive fishes: white perch (*Morone americana*) and round goby (*Neogobius melanostomus*). White perch is a benthopelagic species that can compete with and prey on benthopelagic piscivores

(Schaeffer & Margraf, 1987; Stapanian et al., 2007). Conversely, round goby is a bottom-dwelling species that competes for food and nest habitat with other benthic fishes (French & Jude, 2001), and augments the prey base for piscivores (Johnson et al., 2005). Compositional shifts associated with white perch should therefore be accompanied by declines in benthopelagic piscivores (via competition for shared prey), whereas round goby should reduce benthic fishes (via competition) and increase piscivores (via augmenting prey; Figure 3c). However, older age classes of white perch (age-1+) and all ages of round goby also are known predators on the early life stages of many native fishes (Carreon-Martinez et al., 2014; Roseman et al., 2006; Schaeffer & Margraf, 1987; Steinhart et al., 2004). Both invaders should therefore filter out species with slower life histories (i.e., fewer larger-bodied, longer-lived, later-maturing species) and prolonged egg and larval stages.

By comparing the above predictive framework to observed trait shifts and stressor relationships in each basin (Figure 3a–c), we could infer the relative effects of each stressor on fish compositional

Pool of sentinel fish traits
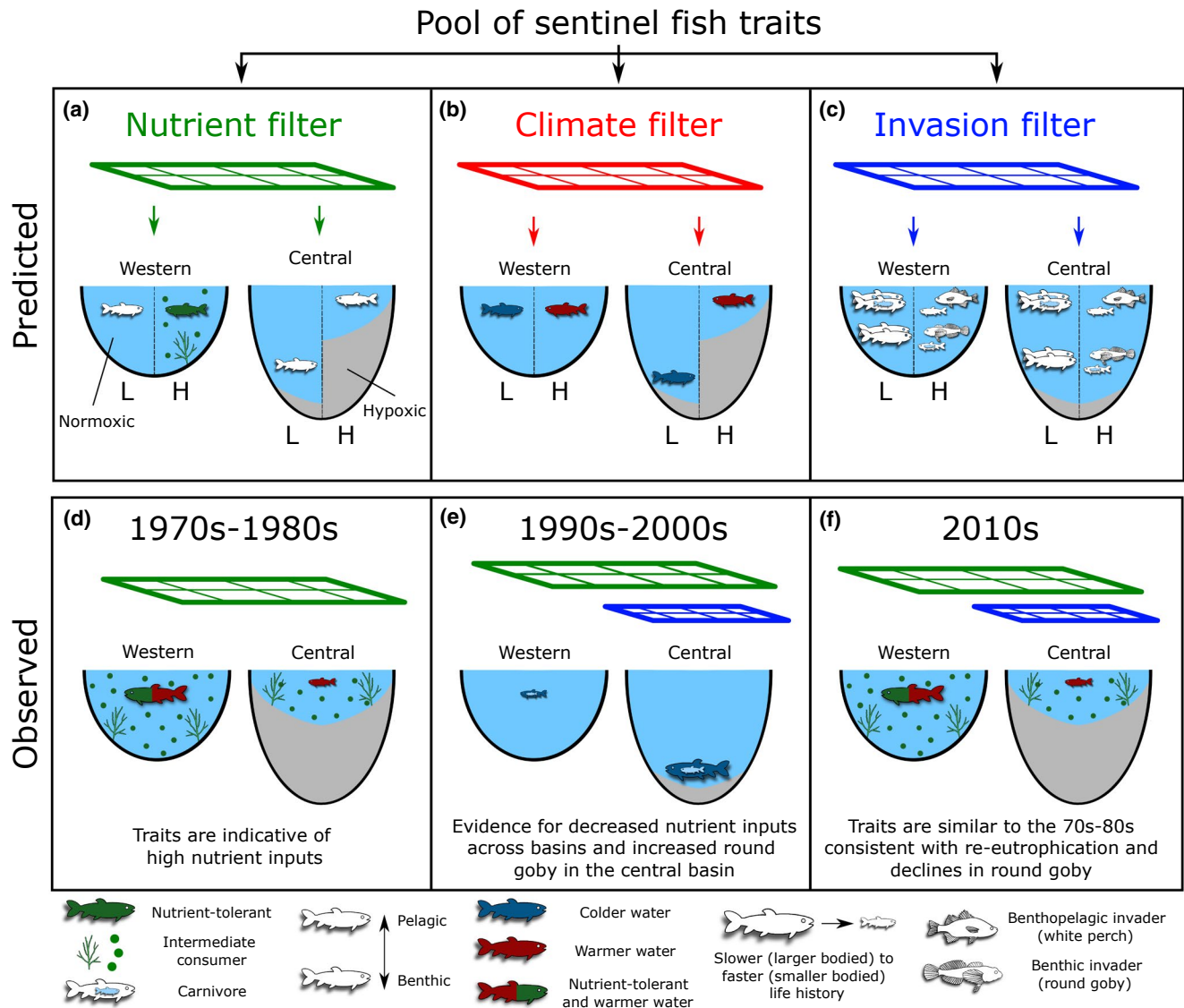
FIGURE 3 Comparisons of (a–c) predicted to (d–f) observed trait changes in response to nutrient inputs, temperature, and invasive species stressors in Lake Erie's western and central basins during 1969–2018, and our summarized interpretations of the dominant stressors in each time period. In panels a–c, "L" represents predictions for absent or low-intensity stressors, whereas "H" represents that stressor at a high intensity. Functional trait values for the sentinel fishes are illustrated using icons that depict traits associated with habitat, feeding, physiology, and life history (see icon legend below the figure). Icons are also used to depict invasive white perch and round goby abundances. Predictions were as follows: (a) increased nutrient inputs would increase pollution-tolerant, intermediate consumers (i.e., detritivores and omnivores) in the western basin and increase benthopelagic fishes in the central basin; (b) water warming would increase fishes from warmer thermal guilds in both basins and increase benthopelagic fishes in the central basin; and (c) invasive white perch would reduce the abundance of benthopelagic, carnivorous species (i.e., piscivores) with a slower life history, whereas invasive gobies would increase carnivores and reduce the abundance of benthic fishes with slower life histories. Study findings were as follows: (d) during the 1970s through 1980s, when nutrient inputs were high and warming and invasion stressors were low, observed trait compositions matched predictions for higher nutrient inputs; (e) During the 1990s through 2000s, as nutrient inputs declined and water warming and invasive fishes increased, trait changes consistently matched predictions for lower nutrient inputs and increased goby abundances, but not increased warming or invasive white perch; and (f) during recent years (2010–2018), changes in trait compositions were similar to past traits associated with higher nutrient inputs and lower goby abundances, with little evidence of trait filtering by warming or white perch. Observed differences in stressor importance are illustrated using present or absent filter icons. Note that climate and invasive fish stressors were considered absent during the 1970s through 1980s

change, including their dependency on environmental (ecosystem) context. Our results highlight the value of combined species and trait perspectives of community change for disentangling multiple stressor effects in one of the world's largest and most perturbed

lakes. These findings also offer useful insights that can aid researchers, resource managers, and conservationists seeking to delineate the independent effects of global, co-occurring stressors in any ecosystem.

2 | MATERIALS AND METHODS

2.1 | Temporal trends in focal anthropogenic stressors

We characterized temporal changes in the stressor conditions of Lake Ere using long-term datasets on nutrient inputs, thermal conditions, and the abundances of white perch and round goby.

Altered nutrient inputs—Lake Erie experienced a period of human-driven eutrophication during the 1950s through 1970s owing to excessive phosphorus inputs from both point (e.g., urban centers) and non-point (e.g., agricultural runoff) sources. Nutrient abatement programs were then adopted in 1972, which helped the lake recover to a more oligotrophic state by the mid-1990s (Makarewicz & Bertram, 1991; Sgro & Reavie, 2018). However, re-eutrophication has occurred in recent decades due to increased non-point phosphorus inputs, particularly from agricultural runoff into lake tributaries (Baker et al., 2019; Scavia et al., 2014; Figure 2b).

We represented these temporal shifts in the trophic state of Lake Erie using an index calculated from point and non-point source phosphorus inputs during 1969–2018. Lakewide point source inputs (metric tons) were obtained during 1974–2018 from Maccoux et al. (2016) and from Great Lakes Blue Accounting (blueaccounting. org). Measurements of point source inputs were not available for 1969–1973. Instead, we estimated point inputs during these years based on the average proportion of total inputs that came from point sources during 1974–1978 (42.8%), given that total phosphorus inputs did not substantially decline until the late 1970s (Sgro & Reavie, 2018). Non-point source nutrient inputs included both total annual bioavailable and non-bioavailable phosphorus loading (metric tons) from the Maumee and Sandusky rivers during 1969–2018. These tributaries are the primary sources of non-point inputs to Lake Erie (Baker et al., 2019; Scavia et al., 2014), with inputs from the Maumee River being most relevant to the western basin and both the Maumee and Sandusky rivers influencing the central basin. Bioavailable and non-bioavailable loadings were calculated following methods detailed in Stumpf et al. (2016) using tributary monitoring data from the National Center for Water Quality Research (ncwqr. org). Monitoring data were available for the Maumee River during 1975–1978 and 1982–2018, and during 1975–2018 for the Sandusky River. To create a complete 1969–2018 dataset for both rivers, we predicted inputs for unmonitored years from river discharge using linear models, given that phosphorus loading tends to be positively related to discharge (Baker et al., 2019).

We created a single nutrient input index for each basin by combining lakewide point source inputs with either non-point source inputs from the Maumee River (western basin) or from the Maumee and Sandusky rivers combined (central basin). Annual point and non-point inputs were first scaled from 0 (minimum) to 1 (maximum) then summed within each year for each basin. This combined metric was then smoothed using a 3-year moving average, with the smoothed values used for 1970–2017 and the unsmoothed values for 1969 and 2018 (see Supporting Information S1 for further details).

We also included data on Secchi disk transparency during 1969–2018 (Figure 2c) in our analyses as an indicator of nutrient-driven changes in the light environment, which affects fish habitat use and feeding ability (Nieman & Gray, 2019). Water transparency (nearest 10 cm) was measured by the Ohio Department of Natural Resources Division of Wildlife (ODNR-DOW) at the same sites that fish were collected (see the invasive species section below and Supporting Information S2).

Climate warming—Climate variability has resulted in a warming of seasonal air temperatures around Lake Erie by an average of about 2.4°C from the mid-1900s to the 2010s (Farmer et al., 2015). To represent this warming trend, we used an index calculated from modeled seasonal surface water temperatures and observed seasonal air temperatures for Lake Erie (Figure 2d). Seasonal lakewide surface temperatures (nearest 0.1°C) during 1969–2018 were calculated from monthly averages provided by the National Oceanic and Atmospheric Administration-Great Lakes Environmental Research Laboratory (NOAA-GLERL; glerl.noaa.gov). These monthly average surface temperatures, which were derived from NOAA-GLERL's Large Lake Thermodynamic Model (Croley & Assel, 1994), were converted to seasonal values by averaging across the months in winter (December–February), spring (March–May), summer (June–August), and fall (September–October). Seasonal air temperatures during 1969–2018 were calculated from daily averages of minimum air temperatures measured at the Toledo, OH airport (ncdc.noaa.gov), which were then averaged across the days within each month and months within each season.

To create a single temperature index, we used principal components analysis to reduce all seasonal surface water and air temperature variables into their principal axes of variation. Only the first principal axis was used, which accounted for most of the total temperature variability (59.8%) and represented an overall shift from cooler to warmer seasonal temperatures through time as axis values increased (see Supporting Information S3 for further details).

Biological invasions—Lake Erie supports numerous invasive fish species, with white perch and round goby being among the most ecologically important given their high abundance after establishment and their potential competitive and predatory impacts on other fishes (Carreon-Martinez et al., 2014; Roseman et al., 2006; Schaeffer & Margraf, 1987; Steinhart et al., 2004). White perch flourished in Lake Erie during the early 1980s (Figure 2e,f), whereas round goby became abundant during the early 1990s (Figure 2g). To represent the temporal trends in these species, we used separate indices for age-0 white perch (juveniles), age-1+ white perch (adults), and all ages of round goby combined with the comparatively rarer, but ecologically similar, tubenose goby (*Proterorhinus semilunaris*). Juvenile white perch were separated from adults to represent their respective competitive (age-0) versus predatory (age-1+) impacts on other fish species.

Abundance indices for these taxonomic groups (Figure 2e–g) were derived from ODNR-DOW trawl survey data collected during fall (mid-September through mid-October) from 1969 to 2018 (see Supporting Information S2 for detailed methods). In brief, these surveys used a stratified sampling design in which six sites in the western basin and

eight sites in the central basin were sampled in each year. Fish abundances in each trawl were standardized to catch-per-unit-effort (CPUE; individuals•trawl min^{-1}) using fishing power corrections to account for differences in catchability (further discussed in Tyson et al., 2006), and averaged across all sites within each basin in each year.

2.2 | Sentinel fish assemblage

One potential issue with using trait changes as direct evidence of stressor effects is that expected trait–stressor relationships can be altered or confounded by other, non-focal interactions (Gravel et al., 2016; Suding et al., 2008). To remove the potential confounding effects of human exploitation (i.e., fishing), and predation by Lake Erie's most abundant native top predator (walleye; *Sander vitreus*), we only used a subset of the Lake Erie fish community in our analyses, which we term "sentinel" species (34 total species; see Table 1). These species have been shown to be sensitive indicators of environmental change because they are only minimally fished (if at all) and are not common or preferred prey of walleye (Ludsin et al., 2001).

We derived abundances of all sentinel fish species using catch information from the same ODNR-DOW fall trawl surveys detailed above. This dataset included the annual averaged abundances (CPUE; individuals•trawl min^{-1}) of all ages of any species that is not a common prey item for walleye and that is not present in the lake in all surveyed years (i.e., its prevalence changes through time; Table 1). We combined some species into broader taxonomic groups owing to potential misidentification of rare or age-0 individuals in the field. For this reason, some abundance indices consist of species grouped at the family-level (e.g., darters), the subfamily-level (e.g., minnows), the genus-level (e.g., crappie), or to individual-level species (Table 1).

2.3 | Functional traits

We focused on functional traits expected to be affected by nutrient inputs, climate warming, and invasive white perch and/or gobies (summarized in Figure 3), which included those associated with functions for habitat use, feeding preferences, reproductive life history, physiology, and body size (detailed in Table 2 and Supporting Information S4). We obtained data on 36 functional traits from the literature and existing databases (e.g., FishBase, fishbase.org; Frimpong & Angermeier, 2009). In some cases, multiple traits were included that describe similar aspects of trait expression, such as traits for both the feeding guild and trophic level of each species. These covarying traits were included to provide multiple lines of evidence for traits with missing information and for traits with less reliable values, such as categorical assessments of habitat use and diet (Cano-Barbacil et al., 2020). For fish species grouped into higher-level taxonomic categories, such as minnows, we used trait data only for the most numerically dominant species in that grouping (denoted in Table 1). Of the 36 compiled traits, we excluded two feeding traits because they exhibited no variance across taxa, and another trait for spawning zone because it varied

too much across taxa to be informative (see Table 2). Additionally, we found four instances in which two or more continuous traits were highly correlated (Pearson's $r > .9$) and described the same function because they detailed either the minimum or maximum values of the same trait, specifically the minimum and maximum of spawn temperature, fecundity, length, and weight. In these instances, we only included a single trait with the fewest missing values. Ultimately, 26 traits remained following these exclusions.

2.4 | Analyses of sentinel species compositional change

We used redundancy analysis (RDA) to quantify sentinel fish species compositional change in relation to our focal anthropogenic stressors (hereafter "predictors") during 1969–2018. This approach is analogous to performing a multiple regression with multivariate response data (Legendre & Legendre, 2012). Separate RDAs were conducted for the western and central basins by relating annual, basin-specific sentinel fish composition (based on annual CPUEs for each taxonomic group) to the annual indices of nutrient inputs, water transparency, temperature, age-0 white perch, age-1+ white perch, and all ages of gobies. None of these predictors exhibited strong collinearity (all variance inflation factors < 2; Dormann et al., 2013) and basin-specific predictors were used if available (see Figure 2). The CPUE values for all taxonomic groups were also log$_{10}$ transformed prior to analyses (Equation 1) following Anderson et al. (2006),

$$x'_{ij} = \log_{10}\left(\frac{x_{ij}}{min(x > 0)}\right) + 1 \quad \text{when } x_{ij} > 0, \tag{1}$$

where x' represents the transformed CPUE for species i in year j and x represents the untransformed CPUE. This transformation preserves zero values and using a higher log base value prioritizes differences in species presence/absence while retaining some weight associated with relative abundance (Anderson et al., 2006). To compare predictors measured in different units, we also transformed each predictor into a z-score by centering it relative to its mean and then dividing it by the associated standard deviation.

We assessed the statistical significance ($p < .05$) of the total variance explained by the anthropogenic predictors and each RDA axis using global permutation tests, and the significance of individual predictors using stepwise permutation tests (Legendre & Legendre, 2012). All RDA analyses were conducted in the R environment (R Core Team, 2020) using the "vegan" package (Oksanen et al., 2019). Global permutation tests were performed with the "anova.cca" function and stepwise permutations tests were performed with the "ordiR2step" function.

2.5 | Analyses of trait compositional changes

We also used RDAs to determine how trait composition varied in relation to the anthropogenic predictors during 1969–2018. We used

TABLE 1 Sentinel fish groups, and the species that form each grouping, in the bottom trawl dataset used to investigate species and trait composition change in the western and central basins of Lake Erie during 1969–2018. An asterisk (*) under the "Common name" heading indicates the dominant species within family-level, subfamily-level, or genus-level groups. Plots of species trends through time are also provided in Figure S2.2

Sentinel fish group (analysis label)	Common name	Scientific name	Number of years present in the dataset	
			Western	Central
Crappie	Black crappie*	*Pomoxis nigromaculatus*	28	12
	White crappie*	*Pomoxis annularis*		
Darters	Blackside darter	*Percina maculata*	10	5
	Channel darter	*Percina copelandi*		
	Greenside darter	*Etheostoma blennioides*		
	Johnny darter*	*Etheostoma nigrum*		
	Sand darter	*Ammocrypta pellucida*		
Minnows	Ghost shiner	*Notropis buchanani*	43	18
	Mimic shiner*	*Notropis volucellus*		
	Sand shiner	*Notropis stramineus*		
	Silver chub*	*Macrhybopsis storeriana*		
Redhorse	Black redhorse	*Moxostoma duquesni*	2	7
	Golden redhorse	*Moxostoma erythrurum*		
	Shorthead redhorse*	*Moxostoma macrolepidotum*		
	Silver redhorse	*Moxostoma anisurum*		
Suckers	Bigmouth buffalo	*Ictiobus cyprinellus*	21	35
	Longnose sucker	*Catostomus*		
	Northern hogsucker	*Hypentelium nigricans*		
	White sucker*	*Catostomus commersonii*		
Sunfish	Bluegill sunfish*	*Lepomis macrochirus*	30	5
	Green sunfish	*Lepomis cyanellus*		
	Orange-spotted sunfish	*Lepomis humilis*		
	Pumpkinseed	*Lepomis gibbosus*		
Whitefish	Lake herring	*Coregonus artedi*	0	22
	Lake whitefish*	*Coregonus clupeaformis*		
Bullhead	Brown bullhead	*Ameiurus nebulosus*	37	0
Burbot	Burbot	*Lota*	2	16
Carp	Common carp	*Cyprinus carpio*	44	32
Catfish	Channel catfish	*Ictalurus punctatus*	49	48
Goldfish	Goldfish	*Carassius auratus*	19	0
Logperch	Common logperch	*Percina caprodes*	39	13
Quillback	Quillback carpsucker	*Carpiodes cyprinus*	32	17
Rock bass	Rock bass	*Ambloplites rupestris*	13	8
Smallmouth bass	Smallmouth bass	*Micropterus dolomieu*	21	NA[a]

[a]Removed from all central basin analyses owing to gear changes that affect the catch of this species (see Supporting Information S2).

the same procedures as detailed above for species composition, except that basin-specific trait compositions were the multivariate response variables in these analyses (see Supporting Information S5: Figure S5.1 for a visual description). We calculated the overall trait composition for each basin by first creating a multivariate "trait space" that represented trait similarities among the different

TABLE 2 List of 36 functional traits analyzed for the sentinel fish assemblages of western and central Lake Erie. Further details on these traits are found in Supporting Information S4 and the trait values for each species are provided in the Supporting Information data appendix (Data S4.1)

Habitat and diet	Primary habitat zone		Maximum spawning temperature[c]
	Primary adult diet		Start month of spawning[b]
	Primary juvenile diet		End month of spawning
	Feeds on detritus		Spawning season
	Feeds on algae or phytoplankton		Median life span (longevity)
	Feeds on macrophytes		Life-history strategy[e]
	Feeds on benthic organisms[a]	Physiology	Preferred temperature[c]
	Feeds on invertebrates or fish larvae[a]		Nutrient pollution tolerance[d]
	Feeds on fish, crayfish, or crabs		Thermal guild
	Feeds at the water surface	Body size (length and weight)	Egg diameter[c]
	Mean trophic level		Lower larval length[c]
	Mouth position		Upper larval length[c]
Reproductive life history	Female age at maturity		Lower adult length[b]
	Minimum fecundity[b]		Upper adult length
	Maximum fecundity		Lower adult weight[b]
	Spawn zone[a]		Upper adult weight
	Serial spawning		Maximum adult length[b]
	Minimum spawning temperature[b,c]		Maximum adult weight[b,c]

[a]Trait not included in multivariate analyses owing to too little or too much variability.

[b]Traits not included in multivariate analyses owing to high correlations with other similar traits.

[c]Traits with a single missing value for one group, genus, or species.

[d]Tolerance of high turbidity and low oxygen (sensu Ludsin et al., 2001).

[e]Calculated following methods from Winemiller and Rose (1992)

sentinel fish taxa. The trait space for each basin consisted of a matrix of pairwise similarities between all present species and their suite of traits. We used Gower's (1971) distance to generate this matrix, which is a non-Euclidean measure appropriate for datasets comprised of a combination of categorical and continuous traits with missing values. To control for trait correlations and ensure that trait similarities were not primarily determined by categories with the most traits, we also weighted the contribution of each trait by the total number of traits in its respective trait category (Pavoine et al., 2009; see Supporting Information S5 for further details). We then used a Cailliez (1983) transformation to make each matrix suitable for Euclidean-based analysis, such as RDA, and decomposed the resulting matrix into its primary axes of variation using Principal Coordinates Analysis (PCoA). From the PCoA for each basin, we calculated annual trait compositions (i.e., the multivariate response variable in the RDAs) as the centroid on each PCoA axis of all sentinel fish taxa present in each basin and year, weighted by their transformed abundances from Equation 1 (a "community-weighted mean"; Lavorel et al., 2008).

To identify which traits were most associated with overall trait compositional shifts, we first identified the two PCoA axes with the highest loadings on RDA axis 1 in each basin-specific analysis (see Supporting Information S5: Table S5.1 for loading values). This first RDA axis captured >75% of the relationship between overall trait composition and the anthropogenic predictors in both basins and thus represented the dimensions of trait space that varied the most in relation to the focal stressors. We then used linear regression to identify which traits were significantly correlated ($p < .05$) with the top two PCoA axes and plotted these traits with overall trait composition in each year to determine which traits primarily changed and in what direction.

We conducted all trait analyses in the R environment (R Core Team, 2020). The Gower distance matrix and trait weights were created using the "gowdis" function from the "FD" package (Laliberté & Legendre, 2010; Laliberté et al., 2014). The PCoAs and community-weighted means were, respectively, calculated with the "pcoa" and "functcomp" functions from the "ape" package (Paradis & Schliep, 2018). Lastly, trait positions on each PCoA axis were calculated

3 | RESULTS

3.1 | Western basin species composition

Temporal changes in the western basin sentinel fish assemblage were best predicted by nutrient inputs, water transparency, temperature, and goby abundance (Figure 4a–d). The significance of these predictors was supported by a global permutation test that included all stressors (explaining 29% of total species variability; $n = 50$, $F_{6,43} = 4.36$, $p = .001$) and by stepwise permutation tests of individual stressors (Figure 4c; Table S5.2). All compositional changes primarily occurred along RDA axis 1, which was the only significant axis ($F_{1,43} = 20.25$, $p = .001$) and represented 77% of the explained variation in sentinel fish composition through time.

During the late 1970s through the mid-1990s, species composition shifted from an assemblage primarily represented by a mixture of common carp, goldfish, bullhead, and crappie to one characterized primarily by minnows (moving rightwards along RDA axis 1; Figure 4a–c). This shift was associated with declines in nutrient inputs as well as increases in water transparency, temperature, and goby abundances. While compositional shifts continued into the 2000s, they were somewhat reversed in the 2010s by declines in the presence of minnows and increases in bullhead, crappie, and quillback (a leftward shift along RDA axis 1; Figure 4a,d). Note, however, that these recent compositional shifts were subtler compared to the larger magnitude shifts that occurred prior to the 1990s, as indicated by their substantially lower horizontal movement along RDA axis 1 (i.e., the primary axis of variation).

3.2 | Western basin trait composition

While shifts in species composition were related to all but one stressor, trait compositional changes were related only to nutrient inputs, water transparency, and goby abundance (explaining 28% of total variability; $n = 50$, $F_{6,43} = 4.23$, $p = .001$; Figure 4e–h). However, despite differences in the important stressors, species and trait composition exhibited similar patterns of temporal change across RDA axis 1 (compare Figure 4a vs. Figure 4e), which was the dominant axis (representing 79% of explained variability; $F_{1,43} = 20.12$, $p = .001$). These similar temporal patterns indicated that the timings of major species changes in the western basin assemblage also corresponded to shifts in trait composition.

Between the late 1970s to the mid-1990s, trait composition changed as nutrient inputs declined and water transparency and goby abundances increased (moving rightward on RDA axis 1; Figure 4e–g). These overall trait compositional shifts on RDA axis 1 corresponded primarily to a rightward movement in trait space on PCoA axis 1, which represented 27.8% of total trait variability in the western basin,

and downward on PCoA axis 3 (13.8%; Figure 5a). The individual traits related to these PCoA axes indicated that trait compositional shifts were associated with losses of warmer-water, pollution-tolerant, intermediate consumers with "slower" life histories (i.e., larger bodied, longer lived, later maturation), such as common carp. Correspondingly, the prevalence of colder-water, pollution-intolerant carnivores with "faster" life histories (i.e., smaller bodied, shorter lived, earlier maturation) increased, such as minnows (Figure 4c). Losses of pollution-tolerant, lower consumers were consistent with our predicted trait responses to declines in nutrient inputs (Figure 3a). Increases in colder-water species (e.g., minnows) during the 1970s through 1990s were the opposite of our expectations for increased warming (Figure 3b). The shift toward faster life histories did match our predictions regarding increased white perch abundance and gobies (Figure 3c). However, no shifts in habitat or diet traits occurred that matched our expectations for these stressors. For example, we expected gobies to increase the prevalence of piscivores, but instead found increases in primarily invertivores (i.e., minnows; Figure 5c).

After the 1990s and into the 2010s, the composition of the western basin sentinel fish assemblage shifted back toward one similar to that of the 1980s (moving leftward along RDA axis 1; Figure 4e–g). The individual traits (and species) associated with this compositional shift during recent decades corresponded to the reverse of those detailed during the 1970s through 1990s (moving leftwards on PCoA 1 and somewhat upwards on PCoA 3 in Figure 5). The increased presence of intermediate consumers that are tolerant of pollution (e.g., bullhead or catfish) matched our predictions for increased nutrient inputs (Figure 3a). These species also tended to have higher thermal preferences, which matched our expectations regarding climate warming (Figure 3b). The shift to slower life histories did match a predicted trait response to declines in white perch and gobies (Figure 3c), but only goby abundances declined during this period (see Figure 2e–g). We observed no other shifts in habitat or diet traits that agreed with our predictions for the effects of invasive fishes (Figures 3c and 5).

3.3 | Central basin species composition

Temporal changes in central basin species composition were most related to nutrient inputs and goby abundance (Figure 6a–d). The significance of these predictors was supported by a global permutation test that included all stressors (explaining 24% of total variability; $n = 50$, $F_{6,43} = 3.53$, $p < .001$) and stepwise permutation tests of individual stressors (Figure 6c; Table S5.2). All compositional changes primarily occurred along RDA axis 1, which was the only significant axis ($F_{1,43} = 16.43$, $p < .001$) and represented 78% of explained compositional variability.

Little compositional change occurred in the central basin until the late 1980s when the presence of crappie declined and burbot, whitefish, minnows, and suckers increased (moving rightwards on RDA axis 1; Figure 6a–c). This shift was associated with declines in nutrient inputs and increases in goby abundance. Afterwards,

Western basin
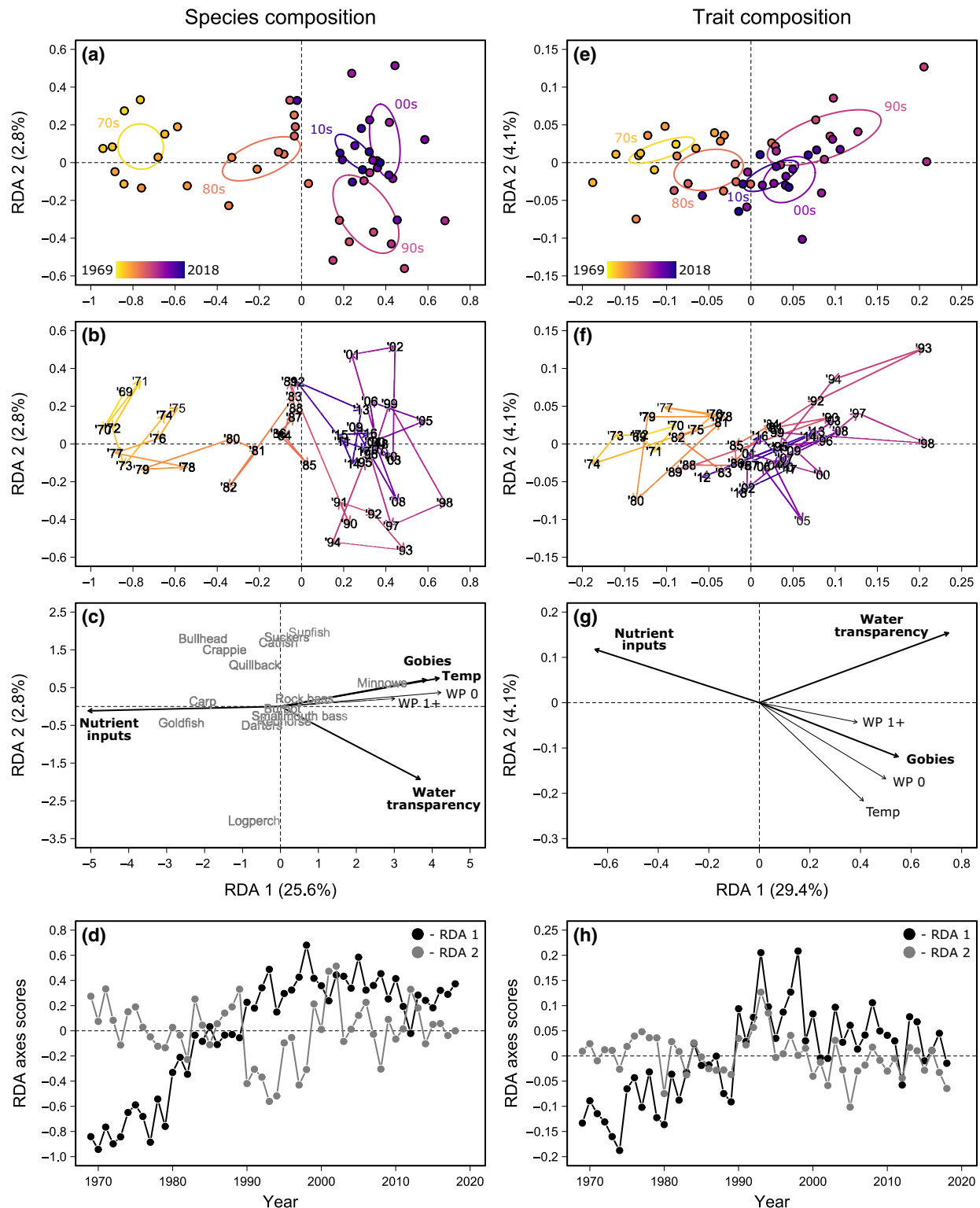
FIGURE 4 Sentinel fish (a–d) species and (e–h) trait composition in Lake Erie's western basin during 1969–2018, based on RDA. Overall patterns in composition are shown in (a, e), with each year progressing across a color gradient from yellow to blue (orange and purple represent intermediate decades). Colored ellipses show the central tendency for each decade, with individual points representing individual years from the 1970s (70s) to 2010s (10s). Year-to-year composition trajectories are in (b, f), with arrow colors progressing across the same yellow to blue color gradient. Environmental predictors (black text) and individual fish taxa (grey text; see Table 2) associated with different regions of the RDA ordination are in (c, g). Bolded black text is used to indicate predictors retained in final RDA models (Temp = temperature; WP 0 = age-0 white perch; WP 1+ = age-1+ white perch). Relationships between time and RDA 1 (black points) and 2 (grey points) axes scores are illustrated in (d, h) to show the exact years associated with large compositional shifts

Western basin
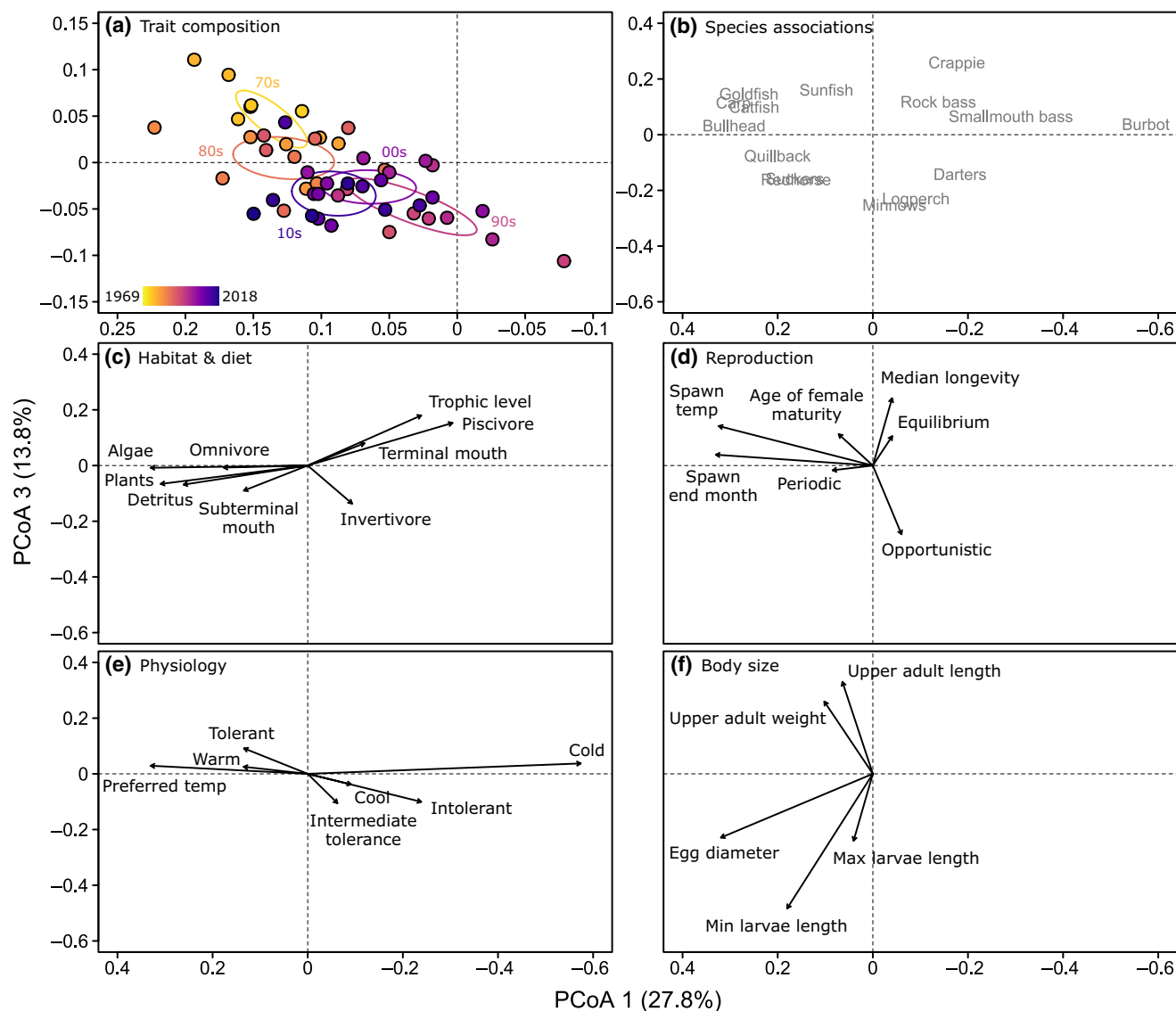
FIGURE 5 Relationships between (a) overall sentinel fish trait composition in Lake Erie's western basin during 1969–2018, (b) the individual species associated with the Principal Coordinates Analysis (PCoA) ordination, and individual trait associations for (c) habitat and diet, (d) reproductive life history, (e) physiology, and (f) body size. In (a), overall trait composition for each year is illustrated as individual points from the 1970s (70s) to 2010s (10s), with each year progressing across a color gradient from yellow to blue (orange and purple represent intermediate decades). Colored ellipses show the central tendency for each decade. Only individual traits that significantly vary (p < .05; based on permutation tests) along PCoA axes 1 or 3 are plotted as black arrows. Also note the reversal of the y-axis, which was done to match the orientation of the ordination in Figure 4, and that arrows are drawn for continuous traits and the separate centroids of each category for categorical traits (e.g., warm, cool, and cold thermal guilds).

around the late 2000s (Figure 6d), burbot and lake whitefish became less common in trawls and catfish and suckers increased (moving leftwards on RDA axis 1; Figure 6a–c).
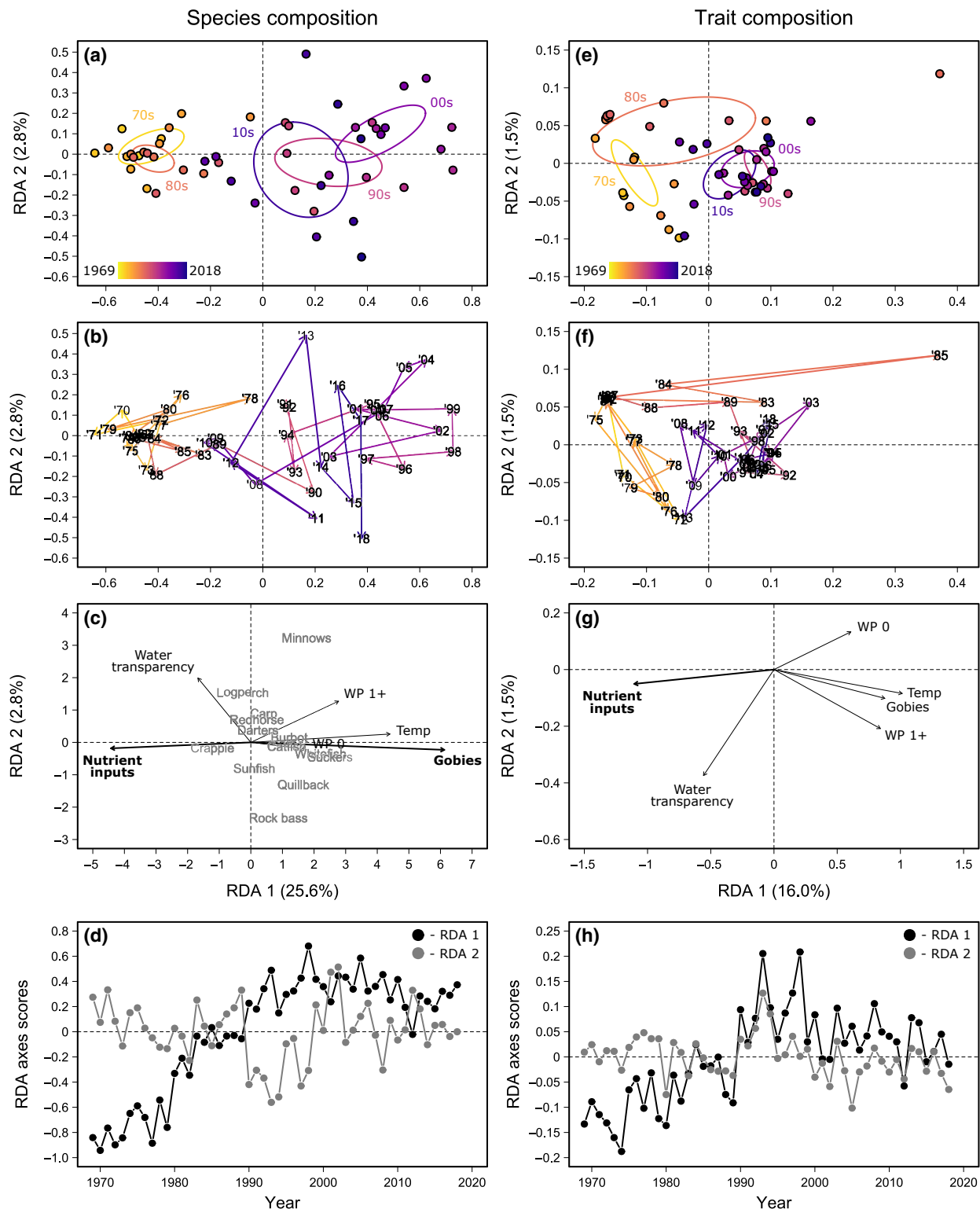
3.4 | Central basin traits composition

The focal anthropogenic stressors explained substantially less variation in trait composition in the central basin (8%; $n = 50$, $F_{6,43} = 1.70$, $p = .049$; Figure 6e–h) compared to the amount explained for species

composition (24%) and for species and trait composition in the western basin (29% and 28%, respectively). This comparatively lower explained variation likely occurred because only a single stressor, nutrient inputs, was related to trait changes in the central basin (Figure 6g; Table S5.2), which contrasts to the importance of multiple predictors in our other compositional analyses.

Temporal changes in trait composition along RDA axis 1 (representing 84% of explained variability; $F_{1,43} = 8.53$, $p = .021$) were similar to those detailed for species composition. Specifically, little consistent community change occurred throughout the 1970s and 1980s until

Central basin

FIGURE 6 Sentinel fish (a–d) species and (e–h) trait composition in Lake Erie's central basin during 1969–2018, based on RDA. Overall patterns in composition are shown in (a, e), with each year progressing across a color gradient from yellow to blue (orange and purple represent intermediate decades). Colored ellipses show the central tendency for each decade, with individual points representing individual years from the 1970s (70s) to 2010s (10s). Year-to-year composition trajectories are in (b, f), with arrow colors progressing across the same yellow to blue color gradient. Environmental predictors (black text) and individual fish taxa (grey text; see Table 2) associated with different regions of the RDA ordination are in (c, g). Bolded black text is used to indicate predictors retained in final RDA models (Temp = temperature; WP 0 = age-0 white perch; WP 1+ = age-1+ white perch). Relationships between time and RDA 1 (black points) and 2 (grey points) axes scores are illustrated in (d, h) to show the exact years associated with large compositional shifts

a pronounced shift occurred around the late 1980s as nutrient inputs decreased (Figure 6e–g). These compositional changes on RDA axis 1 corresponded to shifts rightward in trait space on PCoA axis 1, which represented 29.4% of total trait variability in the central basin, and downward on PCoA axis 3 (14.4%; Figure 7). The individual traits related to these PCoA axes indicated that trait compositional shifts were associated with a reduced presence of benthopelagic, warmer-water, intermediate consumers with faster life histories (e.g., crappie). Correspondingly, benthic, colder-water carnivores with slower life histories, such as burbot and whitefish, increased. Increases in benthic

species agreed with our predictions for lower nutrient inputs into this basin (Figure 3a). Conversely, increases in colder-water, benthic species did not match our expectations for warming (Figure 3b). Some trait changes also matched our expectations for white perch (e.g., more benthic species) or gobies (e.g., more piscivores), but other trait shifts did not. For example, we expected that both invaders would reduce species with slower life histories, but these species actually increased during this period (Figure 3c).

Trait composition in the central basin shifted in a new direction around the late 2000s (Figure 6e–g), which corresponded to

Central basin

FIGURE 7 Relationships between (a) overall sentinel fish trait composition in Lake Erie's central basin during 1969–2018, (b) the individual species associated with the Principal Coordinates Analysis (PCoA) ordination, and individual trait associations for (c) habitat and diet, (d) reproductive life history, (e) physiology, and (f) body size. In (a), overall trait composition for each year is illustrated as individual points from the 1970s (70s) to 2010s (10s), with each year progressing across a color gradient from yellow to blue (orange and purple represent intermediate decades). Colored ellipses show the central tendency for each decade. Only individual traits that significantly vary (p < .05; based on permutation tests) along PCoA axes 1 or 3 are plotted as black arrows. Also note that arrows are drawn for continuous traits and the separate centroids of each category for categorical traits (e.g., warm, cool, and cold thermal guilds)

the reverse of the trait shifts discussed above. The return of benthopelagic, intermediate consumers agreed with our predictions for the effects of increased nutrient inputs in the central basin (Figure 3a). Additionally, the increase in warmer-water, benthopelagic species matched our expectations for warming (Figure 3b). The evidence for effects of white perch and gobies was again mixed. For example, some trait changes matched our expectations for white perch, such as declines in piscivores with slower life histories. Even so, white perch abundances have not changed during recent decades (Figure 2e,f), suggesting this trait shift was not caused by changes in this invader. Similarly, piscivores that prey on gobies declined as goby abundance decreased during this period, which matched our expectations. However, we also anticipated that lower goby abundances would increase benthic species with slower life histories owing to reduced competition and predation, which did not occur.

4 | DISCUSSION

In ecosystems perturbed by multiple simultaneous stressors, discerning which individual or set of stressors is driving community structure is oftentimes difficult. Our results illustrate how supplementing species-based approaches with trait-based ones can help to resolve this issue. By combining analyses of sentinel fish species composition during the past 50 years with shifts in habitat, feeding, reproductive life history, physiological, and morphological traits, we were able to delineate nutrient inputs as a consistent driver of compositional dynamics across both basins. Conversely, we found mixed evidence for the effects of invasive gobies and no consistent correlative or trait-based evidence for the effects of climate warming and invasive white perch. Furthermore, our analyses indicated that some nutrient-related trait changes were influenced by the environmental characteristics of each basin, highlighting a need to consider context-dependent responses when using traits to disentangle multiple stressors. Below, we discuss the insights provided by our approach for teasing apart the effects of co-occurring stressors on the biota of highly perturbed ecosystems such as Lake Erie.

4.1 | Dominant stressors

Stressors associated with nutrient inputs were consistently related to species and trait compositional changes in Lake Erie. Nutrient inputs (including water transparency) were related to temporal species shifts in both basins throughout the 50-year time-series (see Figures 4c and 6c). While trait compositions approximately followed the same temporal patterns as species changes, only nutrient-related predictors were important in both basins, specifically increased water transparency in the western basin and nutrient inputs in the central basin (compare Figures 4g and 6g). The fact that only nutrient-associated predictors were consistently related to both species *and* trait shifts across basins strongly points to nutrient

inputs as the dominant driver of changes in Lake Erie's sentinel fish assemblages during the past half century.

This conclusion was further supported by simultaneous shifts in feeding and thermal traits in relation to changes in nutrient inputs. When nutrient inputs were the predominant stressor during the 1970s, the assemblages of both basins were characterized by warmer-water, intermediate consumers (i.e., detritivores and omnivores), such as common carp and crappies. In this period, lakewide point-source phosphorus inputs averaged ~7800 metric tons and bioavailable inputs from both the Maumee and Sandusky rivers totaled an average of ~640 metric tons (see Figure S1.1). During the 1990s, point-source and bioavailable phosphorus inputs declined (to ~2100 and ~530 metric tons, respectively) and colder-water carnivores (i.e., piscivores and invertivores), such as minnows, burbot, and lake whitefish, became more prevalent. The shift toward more carnivorous species matched our predictions that reduced nutrient inputs would reduce resources for detritivores and omnivores (see Figure 3a; Ludsin et al., 2001). We did not, however, anticipate the associated shift to colder-water species during a period of warming (Farmer et al., 2015; Jones et al., 2006). We suspect that this counter-intuitive result was driven by linkages between thermal and feeding traits, which is supported by the synchronous temporal shifts in these traits. Such a linkage may occur because intermediate consumers in Lake Erie tend to occupy the warmer littoral zones where detritus and plant resources are abundant, and the effects of nutrient inputs tend to be strongest (Thoma & Simon, 2002). High nutrient inputs during the 1970s and 1980s may therefore have favored these warmer-water, intermediate consumers despite the cooler lake temperatures, with these species declining as nutrient inputs decreased into the 1990s even as the lake warmed. This inferred link between thermal and feeding traits was further reinforced by the return of both warmer-water and intermediate consumers during recent decades as bioavailable phosphorus inputs again increased in both basins (from ~530 metric tons in the 1990s up to ~850 during the 2010s). To summarize, the ordinations of species and trait composition in each basin identified nutrient inputs as being consistently important, and comparisons of predicted to observed changes in individual traits (i.e., feeding and associated thermal traits) supported these relationships. This congruence provides multiple lines of evidence that nutrient inputs drove changes in Lake Erie's sentinel fishes and illustrated how combining species with trait perspectives of community change can help to disentangle the actions of co-occurring stressors on animal assemblages.

Combining species and trait approaches also helped to identify potentially spurious relationships between compositional changes and other stressors, such as invasive gobies which were related to species shifts in both basins and trait shifts in the western basin. We predicted that gobies would affect composition by outcompeting other benthic taxa, augmenting prey availability for piscivores, and preying on species with slower life histories. Although increasing goby abundances were related to compositional changes in both basins, we found no evidence for the declines that we expected in benthic taxa that might compete with the gobies during the peak of

the invasion in the mid-1990s and 2000s. This lack of a response in benthic species ruled out the likelihood that gobies were affecting sentinel fish composition via competitive interactions. Piscivores that can consume gobies (e.g., burbot and lake whitefish; Madenjian et al., 2011; Pothoven & Madenjian, 2013) did increase in the central basin during this period, and species with slower life histories declined in the western basin, but these trait shifts were inconsistent across basins. For example, primarily invertivores (i.e., minnows) increased in the western basin and species with slower life histories increased in the central basin. Collectively, the lack of evidence for the competitive effects of gobies and mixed evidence for their role as prey or predators provide little mechanistic support for the effect of this stressor, outside of possibly driving shifts in piscivores in the central basin (represented as the presence of a filter over this basin in Figure 3e,f). Furthermore, even shifts in central basin piscivores could alternatively be explained as a response to changes in nutrient inputs, that is, declining nutrient inputs into the 1990s reduced intermediate consumers and this shift was reversed in recent decades as nutrients increased. Spurious relationships are a notorious problem when relating species changes to environmental predictors (Downes, 2010; Verberk et al., 2013) and our results illustrate how traits can provide mechanistic support (or the lack thereof) for statistical relationships.

Comparisons of our predictions to observed trait changes also proved useful for confirming the lack of effects of invasive white perch and climate warming. We expected white perch to drive declines in benthopelagic piscivores via predation and competition and declines in species with slower life histories through predation. However, we found no consistent shifts in any of these traits following the white perch invasion. In the western basin, sentinel species with slower life histories (e.g., common carp, catfish) did decrease as the abundance of adult white perch increased, but species with slower life histories also increased during recent decades despite no obvious changes in white perch abundance (see Figure 2e,f). Alternatively, for warming, we expected increases in warmer-water species in both basins and benthopelagic fishes in the central basin. Instead, colder-water species (e.g., burbot) increased in both basins and benthic fishes (e.g., burbot and lake whitefish) characterized the central basin trawl catches during the 1990s as the lake warmed. Admittedly, some warmer-water species increased during recent decades (e.g., catfish), which could be partly driven by increased temperatures. Even so, warmer-water thermal guilds also characterized bottom trawls in both basins during the early part of our dataset (1970s to mid-1980s) when the lake was cooler (by about 2.4°C; Farmer et al., 2015), suggesting that the recent increase in warmer-water species may not be indicative of the effects of warming in this ecosystem. These conclusions of the lack of effects of white perch and warming do not necessarily mean that the fishes of Lake Erie are insensitive to these stressors. For example, the recruitment dynamics of other colder-water Lake Erie fishes that are recreationally and commercially fished (e.g., yellow perch, *Perca flavescens*, or walleye) have been shown to be negatively affected by climate warming (Dippold et al., 2020; Farmer et al., 2015). However, these stressor effects could be primarily species specific, or their community-level

impacts have yet to become apparent. We therefore encourage more investigation into the potential population- and community-level effects of these stressors and their impacts on long-term dynamics.

The dominant effects of nutrient inputs in Lake Erie, over that of the other stressors, likely occurred owing to the substantial development within the lake's watershed. Population centers and agriculture are common drivers of eutrophication in aquatic ecosystems (Schindler, 2006; Smith et al., 1999) and Lake Erie is somewhat unique in this regard, compared to the other Great Lakes, due to the presence of multiple, large population centers (i.e., Detroit, Toledo, Cleveland, and Buffalo, USA) and extensive agricultural land use (Host et al., 2019). The greater influence of nutrient inputs in this ecosystem is therefore unsurprising. The strong association between anthropogenic nutrients and compositional changes in Lake Erie, compared to other local (i.e., invasive species) and regional (i.e., climate) stressors, may similarly apply to other waterbodies with extensive human footprints. For example, eutrophication can be a dominant feature in lakes and coastal ecosystems with large, developed catchments (Birk et al., 2020; Lefcheck et al., 2018). Meta-analyses and reviews of stressor interactions in freshwater and marine ecosystems have also shown that nutrients can exhibit a variety of additive and non-additive interactions with other stressors, including warming and invasive species (Crain et al., 2008; Jackson et al., 2016; Smith et al., 2019). Assessing the generality of our results would therefore benefit from further trait-based research that examines the outcome of multiple stressor interactions involving nutrients in different types of aquatic ecosystems and that determines under what conditions nutrient effects dominate.

4.2 | Context-dependent trait responses

Differences in the effects of nutrient inputs between basins also illustrated how some trait responses to the same stressor can vary with ecological context. In the western basin, water transparency was an important predictor of trait changes, with periods of lower water transparency characterized by pollution-tolerant species (i.e., those tolerant of low oxygen and high turbidity; Ludsin et al., 2001) and periods of higher water transparency characterized by less pollution-tolerant species. Conversely, in the central basin, no changes in pollution tolerance occurred, although shifts between benthopelagic and benthic species were evident, which were only related to nutrient inputs. These differing trait shifts and predictor relationships between basins likely occurred owing to their differences in depth and productivity. The western basin is shallower and more eutrophic than the central basin, which tends to result in greater phytoplankton biomass (Watson et al., 2016) and lower water transparency (see Figure 2c) when anthropogenic nutrient inputs are higher. These conditions, therefore, select for fishes tolerant of low water transparency and oxygen (i.e., pollution-tolerant species; Ludsin et al., 2001). By contrast, in the more oligotrophic, deeper central basin, nutrient inputs have more of an effect on the extent and thickness of the hypoxic zone (Rosa & Burns, 1987; Scavia et al., 2014) rather than water transparency (Ludsin et al., 2001), thus explaining why trait changes in this

basin were best predicted by altered nutrient inputs and associated with shifts between benthic and benthopelagic species.

Overall, the differing importance of nutrient-related stressors and trait responses between basins mirrors conclusions from other ecosystems wherein the effects of the same stressor have been shown to depend on environmental conditions (i.e., state or context dependencies; Kroeker et al., 2017; Thrush et al., 2008). This context dependency in trait filtering seems especially relevant for stressors that indirectly select for traits via altered species interactions or habitat conditions (Statzner & Bêche, 2010), such as nutrient inputs which affect communities by altering resource quantity and quality, light levels, and ecosystem chemistry (Smith et al., 1999). Therefore, efforts to disentangle stressors that primarily operate through indirect effects may have to be limited to local scales or single communities because many informative trait responses will be ecosystem specific. Alternatively, efforts to understand stressor impacts across different ecosystems would benefit from focusing on traits that are the least affected by the environmental context, such as the relationships between nutrient inputs and feeding and thermal traits in Lake Erie.

4.3 | Study limitations

In many respects, our trait results were straightforward to interpret due to the dominant effects of nutrient inputs and limited evidence for other stressor effects. However, we were unable to evaluate the effects of other indirect and interacting stressors. For example, while Lake Erie's sentinel fishes are generally not targeted for recreational or commercial fishing, they still compete and interact with other fished species, which could be indirectly influencing species and trait composition. Additionally, although annual data on dreissenid mussels is lacking, we know these invaders colonized the lake during the late-1980s (Hebert et al., 1989) as nutrient inputs declined and goby abundances increased. Dreissenid mussels have contributed to increased light penetration in freshwater ecosystems worldwide, including Lake Erie (Barbiero & Tuchman, 2004), and can be an important food resource for invasive gobies (Barton et al., 2005) and some sentinel fish species (e.g., lake whitefish; Pothoven & Madenjian, 2008). Some trait relationships attributed to increased water clarity and goby abundances may therefore have been partly caused by the dreissenid invasion, albeit not entirely given that trait compositions have shifted during recent decades (see Figures 4 and 6) despite no changes in dreissenid mussel abundances (Strayer et al., 2019). These caveats highlight that, while trait analyses provided valuable insight into the relative effects of our four focal stressors, more long-term monitoring and mechanistic research is needed to address the roles of other historical and emerging stressors in the lake.

4.4 | Conclusions

Disentangling multiple stressor interactions is crucial for understanding and managing aquatic and terrestrial communities impacted by anthropogenic environmental change (Côté et al., 2016; Downes, 2010). Such knowledge can help researchers, resource managers, and conservation agencies to (i) understand the past dynamics of their focal communities, (ii) forecast the effects of ecosystem change, (iii) identify rehabilitation or conservation strategies, and (iv) set appropriate expectations for user groups and stakeholders (Côté et al., 2016; Dippold et al., 2020; Smith et al., 2019). In this study, quantifying the association of multiple anthropogenic stressors with species and trait composition revealed a dominant role of nutrients (with potentially a secondary influence of invasive gobies) over that of climate warming and invasive white perch. This conclusion was also supported by comparisons of predicted trait responses to observed changes in individual traits for habitat use, feeding preferences, reproductive life history, physiology, and body size, thus providing multiple lines of evidence for which trait–stressor relationships were likely causative. Our investigation also provided new insights into the degree to which trait responses are generalizable and indicated that care must be taken when selecting traits to identify stressor effects across different communities or ecosystems. Ultimately, our study highlights the value of combining species and trait perspectives of community change to better delineate the independent effects of multiple stressors, which can be used to support conservation and management efforts aimed at sustaining valued populations.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All trait data used in our analyses are provided in Supporting Information S4. All taxa abundance and anthropogenic stressor data are publicly available from the Dryad digital repository at https://doi.org/10.5061/dryad.2bvq83br4.

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