Received: 1 June 2023 | Accepted: 25 August 2023

DOI: 10.1002/ecy.4173

ARTICLE

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Biological invasions alter the structure of a tropical freshwater food web

Diana M. T. Sharpe[1,2,3] | **Marisol P. Valverde**[2,4] | **Luis F. De León**[3,5,6] | **Andrew P. Hendry**[2] | **Mark E. Torchin**[3]

[1]Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts, USA

[2]Department of Biology, McGill University, Montréal, Québec, Canada

[3]Smithsonian Tropical Research Institute, Panama City, Panama

[4]Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, New York, USA

[5]Department of Biology, University of Massachusetts Boston, Boston, Massachusetts, USA

[6]Instituto de Investigaciones Cientificas y Servicios de Alta Tecnologia, Centro de Biodiversidad y Descubrimiento de Drogas, Panama City, Panama

Correspondence
Diana M. T. Sharpe
Email: diana_sharpe@fas.harvard.edu

Funding information
NSERC CREATE in Biodiversity Ecosystem Services and Sustainability, BESS; National Geographic Society, Grant/Award Number: 3221-4; SENACYT, Grant/Award Number: ITE12-002; Sistema Nacional de Investigadores de Panama

Handling Editor: Michale Monoghan

Abstract

Biological invasions are expected to alter food web structure, but there are limited empirical data directly comparing invaded versus uninvaded food webs, particularly in species-rich, tropical systems. We characterize for the first time the food web of Lake Gatun—a diverse and highly invaded tropical freshwater lake within the Panama Canal. We used stable isotope analysis to reconstruct the trophic structure of the fish community of Lake Gatun and to compare it to that of a minimally invaded reference lake, Lake Bayano. We found significant differences between the trophic structures of these two Neotropical lakes, notably that Lake Gatun's fish community was characterized by a longer food chain, greater isotopic diversity, a broader range of trophic positions and body sizes, and shifts in the isotopic positions of several native taxa relative to Lake Bayano. The degree of isotopic overlap between native and non-native trophic guilds in Lake Gatun was variable, with herbivores exhibiting the lowest (20%–29%) overlap and carnivores the greatest (81%–100%). Overall, our results provide some of the first empirical evidence for the ways in which multiple introduced and native species may partition isotopic space in a species-rich tropical freshwater food web.

KEYWORDS
food webs, invasive species, isotopic niches, stable isotope analysis, trophic structure, tropical lakes

INTRODUCTION

A central goal in ecology is to understand the mechanisms that influence the size and structure of food webs (Polis & Winemiller, 2013). One major influence on contemporary food webs is the addition of non-native species via human-mediated introductions. Introduced species can influence the abundance, distribution, behavior, and trophic ecology of native species and, thus, can alter both the nodes and links of food webs, resulting in

complex changes in overall food web structure in invaded systems (David et al., 2017; Jackson et al., 2017; Sagouis et al., 2015). Freshwater ecosystems provide interesting systems to explore these effects, as they tend to be heavily invaded and have also been frequently used as model systems to develop and test theory in trophic ecology (Jackson et al., 2017).

Rigorously quantifying invader impacts at the whole food web level requires directly comparing an entire food web before versus after invasion and/or comparing similar food webs that vary in the level of invasion; however, a recent systematic review concluded that such studies were "exceedingly rare" (David et al., 2017). Indeed, to our knowledge, only five studies have tested for the consequences of invasions in freshwater systems at the food web scale (Amundsen et al., 2013; Britton et al., 2010; Ozersky et al., 2012; Vander Zanden et al., 1999; Wainright et al., 2021; Woodward & Hildrew, 2001)—and all of these focused on temperate ecosystems. These studies found evidence for marked changes in food web structure following invasion, including increases in food chain length (Walsworth et al., 2013; Woodward & Hildrew, 2001) and overall isotopic niche breadth (Rogosch & Olden, 2020; Wainright et al., 2021).

The lack of comparative food web studies from the tropics limits our understanding of the global consequences of invasions given that the diversity of both native (Lévêque et al., 2008) and introduced (Sax, 2001) fishes varies with latitude. There is also evidence that biotic resistance toward non-native species may be stronger in the tropics (Freestone et al., 2013), so we might expect the food web consequences of invasions to be very different in species-rich tropical assemblages than they are in more depauperate temperate lakes. The Neotropics in particular are home to the most taxonomically and functionally diverse fish fauna in the world (Albert et al., 2020; Toussaint et al., 2016), yet a review of 45 studies that examined the trophic consequences of freshwater fish invasions found that only 2% were conducted in the Neotropics (Cucherousset et al., 2012).

Here, we seek to address this gap by characterizing the food webs of two large Neotropical lakes that vary in their level of invasion. We compared the isotopic structure of a highly invaded fish community (Lake Gatun; with 16 non-native species) to that of a minimally invaded reference lake (Lake Bayano, with only a single non-native fish species). Both lakes have a similar history of impoundment and similar morphometry and physiochemical variables (Sharpe et al., 2017), and their native communities derive from rivers with similar freshwater fish faunas (Meek & Hildebrand, 1916; Smith & Bermingham, 2005).

The unique invasion history and biogeographical context of this system make it a good model for exploring how novel food webs are structured when multiple species with little or no coevolutionary history begin interacting with one another. Lake Gatun was formed by the damming of the Chagres River in 1914, which bridged the continental divide and brought the historically separate Atlantic and Pacific freshwater fish faunas into secondary contact (Meek & Hildebrand, 1916; Smith et al., 2004). The lake was initially colonized by native riverine species from the Rio Grande and Chagres watersheds, leading to a rich assemblage of native freshwater fishes (Breder, 1944). The newly formed Lake Gatun also formed part of the Panama Canal—one of the world's major interoceanic shipping routes. This has allowed for multiple freshwater-tolerant marine and estuarine species from both the Atlantic and Pacific oceans to disperse into Lake Gatun over the past century (Castellanos-Galindo et al., 2020; Cohen, 2006; Hildebrand, 1939). Finally, between the 1960s and 1990s, multiple non-native freshwater fishes were intentionally introduced for aquaculture or fishing (Gonzalez, 1995), most notably the predatory Peacock bass (*Cichla monoculus*), which had dramatic and long-lasting effects on the diversity and structure of the native fish community (Sharpe et al., 2017; Zaret & Paine, 1973). Although efforts have been made to document these invasions (Castellanos-Galindo et al., 2020; Guiterrez et al., 1995; Schreiber et al., 2023; Sharpe et al., 2017) and to understand their impacts on community structure (Sharpe et al., 2017; Zaret & Paine, 1973), their consequences for the food web remain unexplored.

To empirically compare the food webs of these two lakes, we use stable isotope analysis (SIA)—an approach that infers trophic relationships among species from measurements of the ratios of carbon and nitrogen isotopes in their tissues (Fry, 2006; Peterson & Fry, 1987). SIA is now widely used to visualize food web structure (Layman et al., 2012), study trophic niches (Bearhop et al., 2004; Newsome et al., 2007), and quantify food web responses to perturbation (Layman et al., 2005; Layman, Quattrochi, et al., 2007). We posed the following questions: (1) How does trophic structure (food chain length, isotopic niche breadth, trophic position [TP] and body size distributions) differ between a minimally invaded (Bayano) versus heavily invaded (Gatun) assemblage? (2) To what extent do native and non-native trophic guilds overlap in isotopic niche space? (3) How do the TPs of native species shift between lakes?

METHODS

Study sites and field collections

Our study focused on lakes Gatun and Bayano, located approximately 120 km apart in central Panama (Appendix S1: Figure S1). Both are artificial reservoirs

and are similar in terms of morphometry, physiochemical parameters, and original freshwater fish faunas, but differ in invasion history, with Gatun having at least 16 non-native fishes and Lake Bayano having only one (Appendix S1: Tables S1–S3). Gatun's non-native fishes include freshwater fishes stocked for aquaculture and recreational fishing between the 1960s and 1990s, as well as marine species that appear to have migrated from the ocean through the locks, most of which began regularly appearing in catches in Gatun after 2013 (Appendix S1: Table S2). Some of these marine species have established permanent breeding populations in Gatun (e.g., *Microphis lineatus* [Breder, 1944]), but it remains unclear whether or not the majority breed in the lake.

Fish and invertebrates were collected between 2013 and 2018 using a variety of gear, including multipanel experimental gill nets, beach seines, cast nets, minnow traps, baited bottle traps, and angling (see Appendix S1 and Sharpe et al., 2017 for details). All field samples were collected with permission from Panama's Ministerio del Ambiente (Permit nos. SE/AP-21-13, SC/A-29-13, SE/AP-11-15, and SE/AP-40-15), and all handling of live vertebrates was done in compliance with the Smithsonian Tropical Research Institute's (STRI) Institutional Animal Care Committee (IACUC Protocol nos. 2013-0507-2016, 2016-0224-2019). We collected surface-grazing snails (*Pomacea* sp. and *Melanoides tuberculata*) and filter-feeding bivalves (*Anodonta luteola*, *Corbicula fluminea*) to characterize the base of littoral and pelagic food webs, respectively (Cabana & Rasmussen, 1996; Post, 2002). Fish were classified by trophic guild (herbivores, omnivores, and carnivores; Appendix S1: Table S4) and by origin (native, marine, or introduced; Appendix S1: Table S2). We considered both of the latter categories (marine and introduced) to be "non-native," as they both gained access to the lake via anthropogenic vectors.

Food web reconstruction

The trophic structure of the fish communities of both lakes was reconstructed using SIA. Muscle tissues were dissected, ground, and dried following standard protocols (Appendix S2). Isotopic ratios (δ^{13}C and δ^{15}N) were measured with a mass spectrometer and are reported using δ (delta) notation, where

$$\delta^{13}\mathrm{C}\ \text{and}\ \delta^{15}\mathrm{N} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1\right) \times 1000,$$

where R is the ratio of ^{13}C:^{12}C or ^{15}N:^{14}N, and the standards are Pee Dee Belemnite for carbon and atmospheric nitrogen for N. Isotopic baselines differed across lakes (Appendix S2: Figures S2 and S3), and so δ^{15}N values of all fishes were corrected to facilitate more direct comparisons between the two food webs, as follows:

$$\delta^{15}\mathrm{N}_{\text{adj}} = \delta^{15}\mathrm{N}_i - \delta^{15}\mathrm{N}_{\text{baseline}},$$

where $\delta^{15}N_i$ is the raw (unadjusted) isotopic values for the ith individual, and $\delta^{15}\mathrm{N}_{\text{baseline}}$ is the lake-wide mean δ^{15}N of primary consumers (mean δ^{15}N for pelagic and littoral primary consumers, respectively, were similar for Gatun [6.40 ± 0.14 vs. 6.41 ± 0.22] and Bayano [3.12 ± 0.08 vs. 3.69 ± 0.22]). There was no significant ontogenetic variation for the majority of fish species examined (Appendix S2: Figures S4 and S5), suggesting that our sampling approach (of targeting only adults) was largely effective at controlling for this potential confounding factor (see Appendix S2 for details). We also examined the magnitude of interannual variation in isotopic signatures (Appendix S2: Figures S6–S8). We found that relationships among species remained consistent through time, and years were therefore pooled in all subsequent analyses.

We used the Stable Isotope Bayesian Ellipses (SIBER) package in R (Jackson et al., 2011) to estimate the isotopic niche widths of native, introduced, and marine trophic guilds (Appendix S2: Table S1) and to estimate the overall isotopic niche breadth of each food web using community-wide metrics (Layman et al., 2007). These included (1) δ^{15}N range (NR), which provides an estimate of the vertical structure within a food web; (2) δ ^{13}C range (CR), which provides an estimate of the variety of basal resources exploited; (3) total convex hull area (TA); and (4) mean distance to centroid (CD), where both of the latter two metrics provide an overall measure of trophic diversity within the food web.

We estimated the TP of each fish species (Jepsen & Winemiller, 2002; Post, 2002) using the equation

$$\mathrm{TP} = \lambda + \frac{\left(\delta^{15}\mathrm{N}_i - \delta^{15}\mathrm{N}_{\text{baseline}}\right)}{\Delta_n},$$

where λ is the TP of the organisms used to estimate $\delta^{15}\mathrm{N}_{\text{baseline}}$, in this case two for primary consumers (gastropods and bivalves); $\delta^{15}\mathrm{N}_{\text{baseline}}$ is the mean δ^{15}N of primary consumers, measured directly; and Δ_n is trophic fractionation rate. We used a fractionation rate of 2.54‰, which was the mean from 134 controlled studies (Vanderklift & Ponsard, 2003). The food chain length of each lake was estimated as the maximum TP.

We visualized trophic structure by plotting mean TP for each species (estimated from our isotopic data, see above) against mean body size and relative biomass

(estimated from our 2013–2015 field surveys; see Sharpe et al., 2017 and Appendix S2 for details). Finally, we compared the baseline-adjusted isotopic signatures ($\delta^{15}N_{adj}$) of all native, freshwater taxa that were present in both lakes using *t*-tests or Wilcoxon tests (see Appendix S2 for details).

RESULTS

Stable isotope biplots revealed key differences in overall trophic structure between Lake Bayano (14 species with one non-native species, ca. 7%) and Lake Gatun (29 species with 16 non-native species, ca. 55%; Figure 1). In Lake Bayano, native fishes were relatively tightly clustered in isotopic space, resulting in a relatively small native convex hull area (Figure 1a). The native pike characid *Ctenolucius beani*, a piscivore, was the most $\delta^{15}N$-enriched, and the native herbivore, *Cyphocharax magdalenae*, had the lowest mean $\delta^{15}N$ (Figure 1a). Lake Bayano contained a single introduced fish, the herbivorous Nile tilapia, *Oreochromis niloticus*, which clustered closely in isotopic space with the native herbivore *C. magdalenae* (Figure 1a). The core isotopic niche (SEAc) of native herbivores in Lake Bayano overlapped to a moderate degree with that of the single introduced herbivore, *O. niloticus* (Figure 2a).

In Lake Gatun, native species were more widely dispersed in isotopic space, resulting in a much larger native convex hull area than Lake Bayano (Figure 1b). The food web for Lake Gatun also contained 16 novel species, of which seven were introduced freshwater species and nine were marine species that entered the lake through the Panama Canal locks (Castellanos-Galindo et al., 2020; Sharpe et al., 2017). In terms of their trophic guilds, 11 were carnivores, four were herbivores, and one was an omnivore. Isotopic means for the majority (nine out of 16) of these non-native species were located either on the periphery, or outside, of the isotopic niche space occupied by native species (Figure 1b). For example, six marine carnivores (the anchovy *Anchoa parva*, the fat snook *Centropomus parallelus*, the swordspine snook *C. ensiferus*, the common snook *C. undecimalis*, the yellow jack *Caranx* sp., and the tarpon snook *C. pectinatus*)

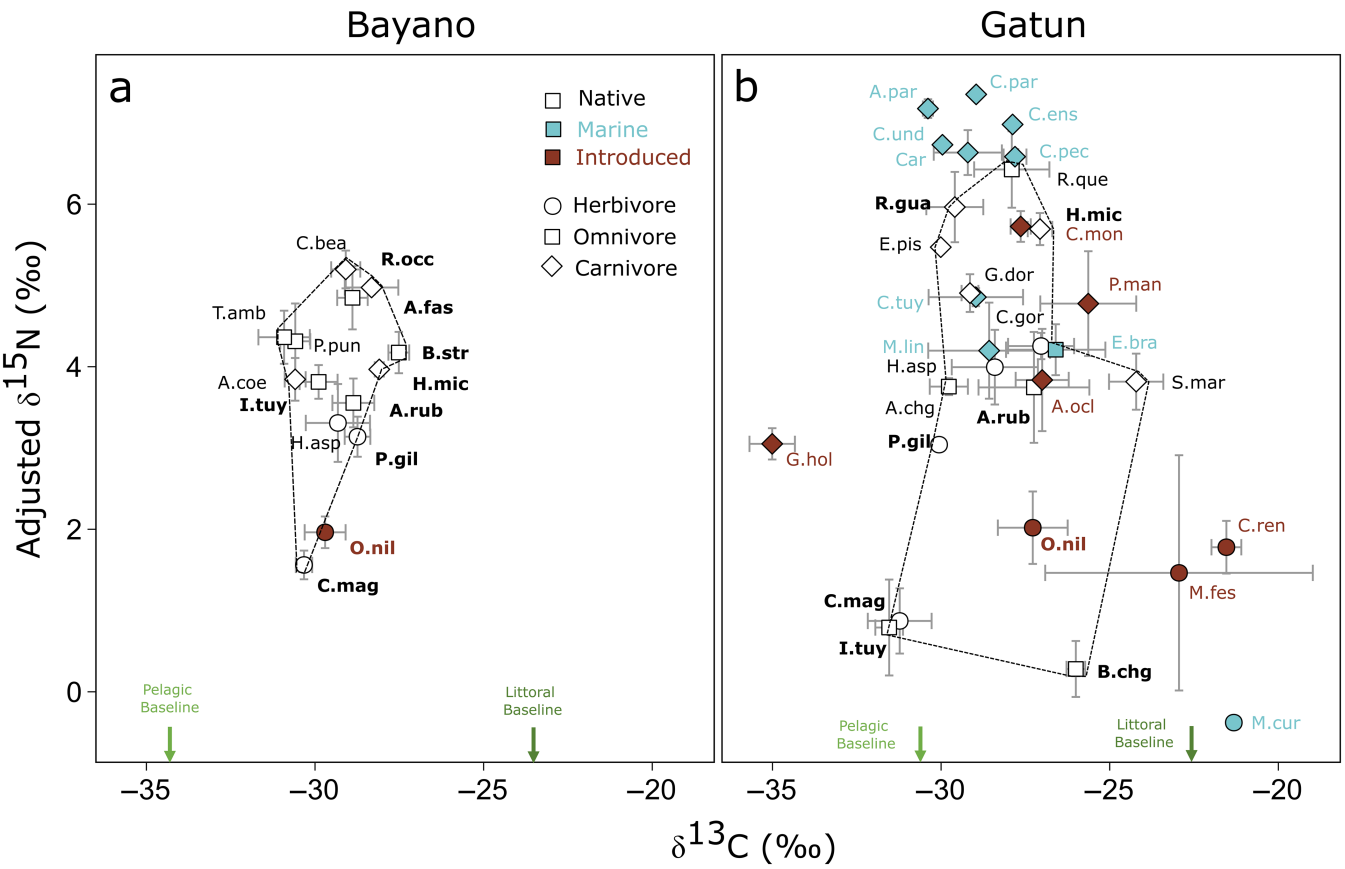

FIGURE 1 Stable isotope biplots for Lakes Bayano (a) and Gatun (b). Data shown are mean (±1 SE) adjusted $\delta^{15}N$ (‰) and $\delta^{13}C$ (‰) for all species of fish sampled, grouped by trophic guild and by origin. Please see Appendix S1: Table S2 for species codes. Species and genera that are common to both lakes are in bold. The dashed line is a convex hull polygon around the native fish community. The pelagic and littoral baselines are the mean $\delta^{13}C$ values of bivalves and snails, respectively.

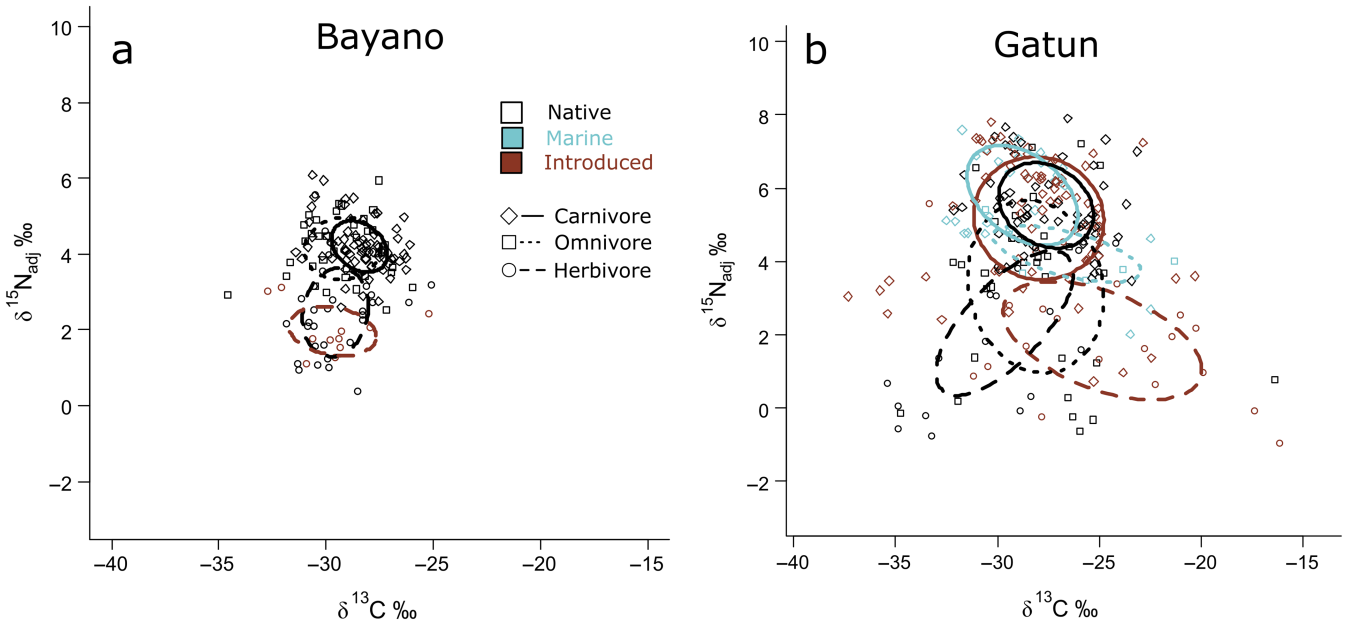

FIGURE 2 Core isotopic niches of the major trophic guilds of fishes in Lakes Bayano (a) and Gatun (b). Data points are isotopic values of individual fish, coded by trophic guild and by origin. Ellipses represent the standard ellipse area—an estimate of the core isotopic niche that encompasses approximately 40% of data points.

were more δ^{15}N-enriched than all native freshwater carnivores. In addition, the non-native herbivores (the redbreast tilapia *Coptodon rendalli*, the flag cichlid *Mesonauta festivus*, and the white mullet *Mugil curema*) were more enriched in δ^{13}C than all native herbivores (Figure 1b).

At the level of entire trophic guilds, there was a high degree of overlap in Gatun in the core isotopic niches (SEAc) of native, marine, and introduced carnivores (Figure 2b). However, this overlap was asymmetrical, with native carnivores experiencing the highest degree of overlap (Figure 3a), both from marine carnivores (81% overlap) and introduced freshwater carnivores (100% overlap). In contrast, introduced freshwater carnivores experienced the lowest degree of overlap (Figure 3c), with only 41% overlap from native carnivores and 53% from marine carnivores. Marine carnivores experienced an intermediate level of overlap (Figure 3b), with 62% overlap with native carnivores and 81% overlap with introduced carnivores. There was low niche overlap among the herbivores in Lake Gatun, with native and introduced herbivores showing 20% and 29% isotopic niche overlap, respectively. Indeed, there was clear niche partitioning among Gatun's herbivores along the δ^{13}C axis. Native herbivorous fishes (*C. magdalenae*, *Hemiancistrus aspidolepsis* and *Poecilia gilli*) were more depleted in δ^{13}C, suggesting a greater reliance on pelagic primary production. In contrast, introduced/marine species (*O. niloticus*, *C. rendalli*, *M. festivus*, and *M. curema*) were more enriched in δ^{13}C, suggesting a greater reliance on littoral carbon sources (Figures 1b and 2b).

The fish community of Lake Gatun had a longer food chain (length = 4.89) than that of Lake Bayano (length = 4.05). Community-level indices revealed greater isotopic diversity for fishes in Lake Gatun relative to Lake Bayano (Appendix S2: Figure S9). Specifically, Gatun's fish community spanned a broader range of δ^{15}N and δ^{13}C (Appendix S2: Figure S9a,b) values relative to Bayano. As a result, the fish community of Gatun as a whole occupied a much broader isotopic niche space, which was reflected in a larger total convex hull area and greater mean distance to centroid (Appendix S2: Figure S9c,d) relative to Lake Bayano.

There were striking differences in the distribution of TPs and the size structure of the fish communities of Lakes Bayano and Gatun (Figure 4). Lake Bayano had only a single consumer with a TP greater than 4 (*C. beani*) and relatively few large-bodied species. Native omnivores and herbivores (*Brycon striatulus* and *C. madgalenae*) were a dominant component of the biomass (Figure 4a). In contrast, Lake Gatun contained many more large-bodied and higher-trophic-level species than Bayano (note upper-right quadrant of Figure 4), many of which were non-native. Notably, the six species at the top of Gatun's food web were all marine: *C. parallelus* (TP = 4.89), *A. parva* (TP = 4.83 ± 0.04), *C. ensiferus* (TP = 4.75), *C. undecimalis* (TP = 4.65), *Caranx* sp. (TP = 4.61 ± 0.10), and *C. pectinatus*

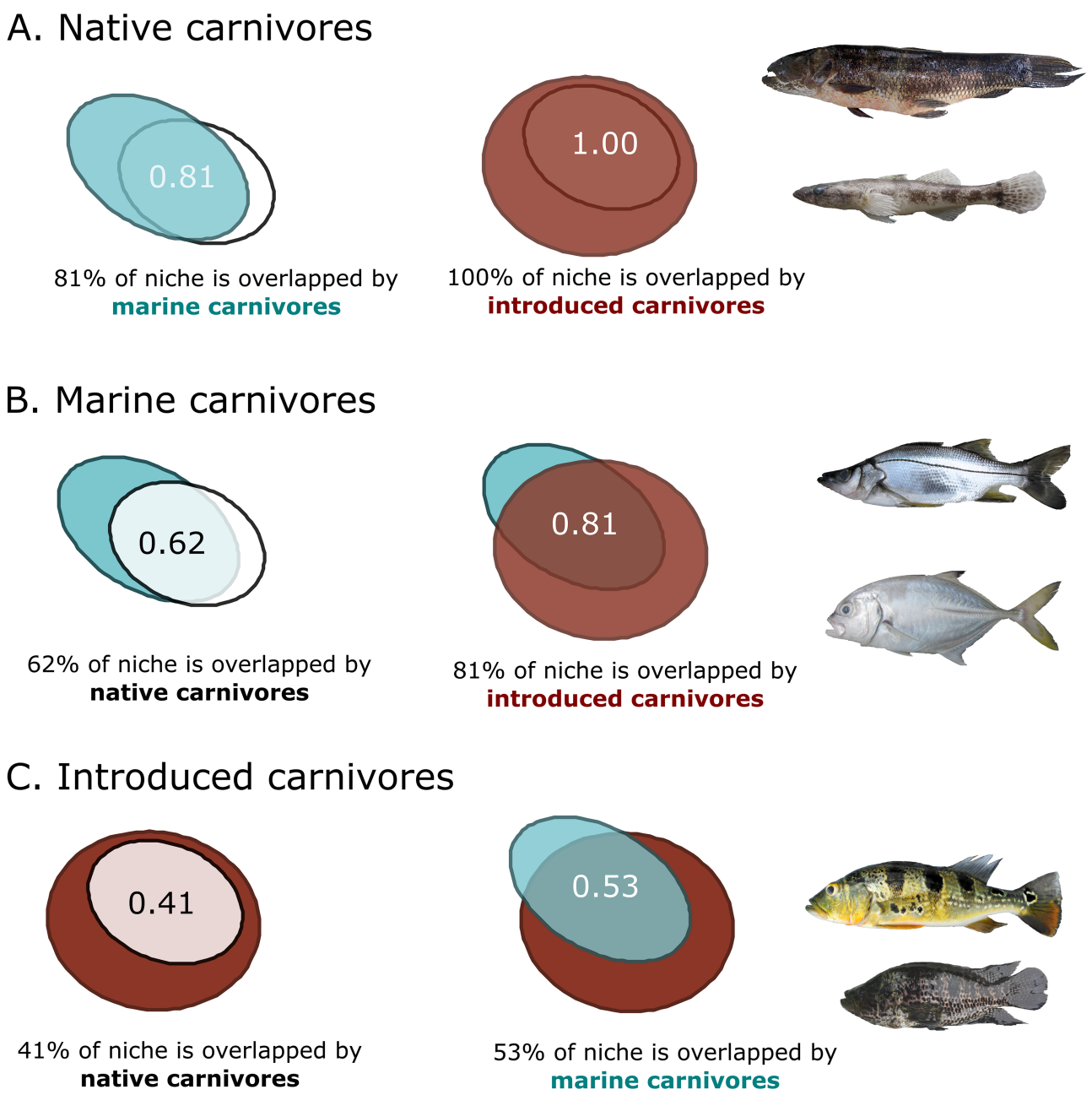

FIGURE 3 Pairwise isotopic niche overlap between native freshwater (a, white), marine (b, light blue), and introduced (c, dark red) carnivores in Lake Gatun. Ellipses (extracted from Figure 2) are the standard ellipse area (SEA), an estimate of the core isotopic niche that encompasses approximately 40% of data points. Numbers on the ellipses represent the proportional overlap (from 0 to 1) between each pair shown, based on their SEAc (standard ellipse area corrected for small sample sizes). Representative species shown are (top to bottom) *Hoplias microlepis* and *Gobiomorus dormitor* (a), *Centropomus* sp. and *Caranx* sp. (b), and *Cichla monoculus* and *Parachromis managuensis* (c). Photo credits: Diana M. T. Sharpe.

(TP = 4.59 ± 0.03). Large-bodied introduced carnivores (Peacock bass, *C. monoculus*, the jaguar cichlid *Parachromis managuensis*, and the Oscar, *Astronotus ocellatus*) and the introduced *O. niloticus* were among the greatest contributors to community biomass (Figure 4b). Finally, introduced and marine species spanned all trophic levels and size classes (Figure 4b). For example, the smallest-bodied fish in our data set was the introduced insectivore *Gambusia holbrooki*, and the species with the lowest TP in the food web was the white mullet, *M. curema*—a marine fish (TP = 1.85).

Three native freshwater taxa exhibited shifts in isotopic position between the minimally invaded (Bayano) and highly invaded context (Gatun). The native piscivore *Hoplias microlepis* was enriched on average by 1.73‰ in $\delta^{15}N$ in Gatun relative to Bayano ($W = 170$, $p < 0.001$),

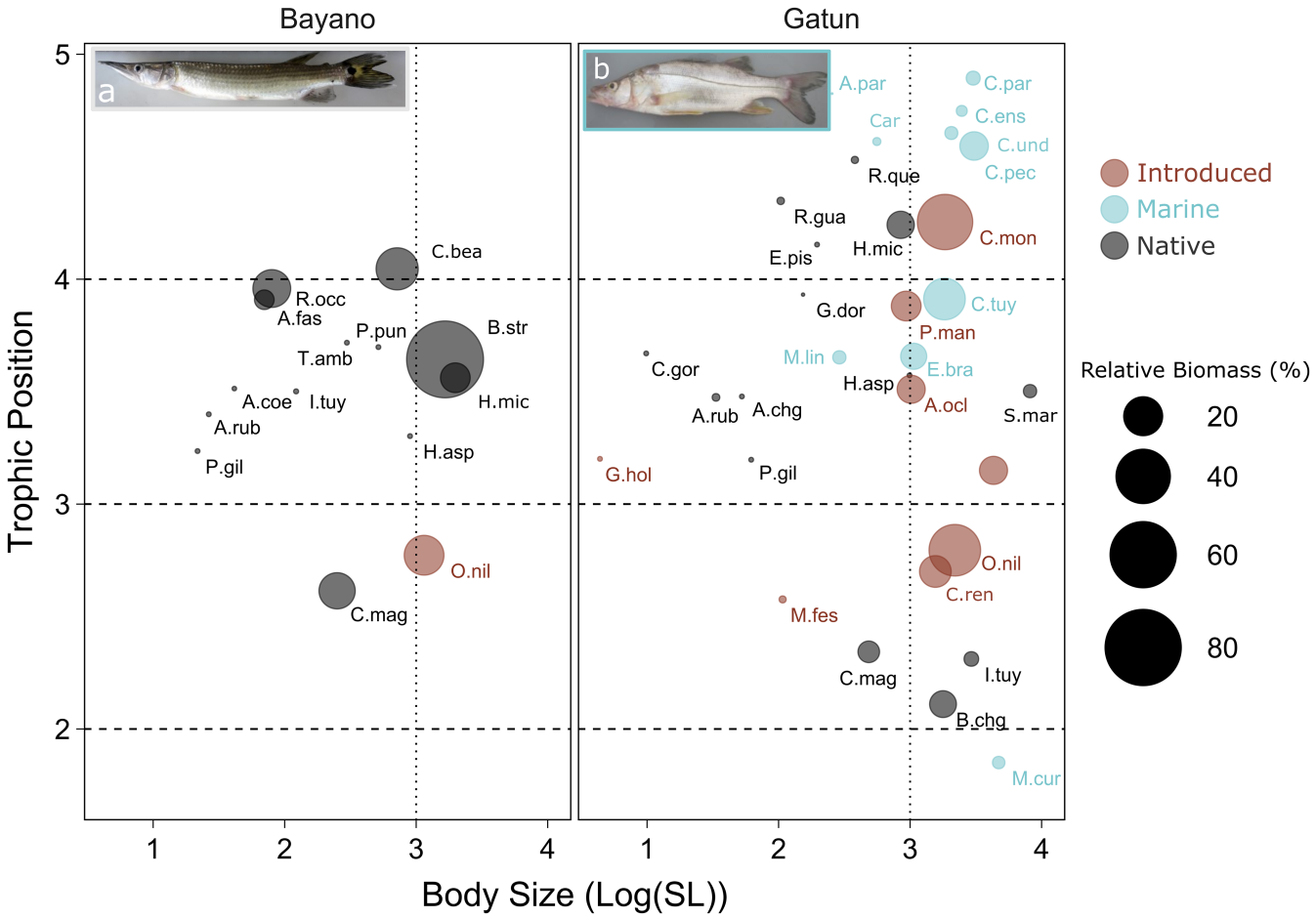

FIGURE 4 Trophic and size structure of fish communities of Lakes Bayano (a) and Gatun (b). Data points show the mean trophic position (calculated from isotopic data) and body size (log-transformed mean standard length [in centimeters]) of each fish species. The size of each circle is scaled to represent the relative biomass (in percentage) of that species in the lake, based on data from standardized gill-net surveys conducted from 2013 to 2015 (Sharpe et al., 2017). Species that were not captured in gill nets, and thus are lacking biomass estimates, are represented by a point only. The apex consumer in Bayano is the native freshwater characid *Ctenolucius beani* (inset in panel a) and in Gatun the marine snook, *Centropomus parallelus* (inset in panel b). Photo credits: Diana M. T. Sharpe.

which corresponds to an increase of roughly 0.70 trophic levels (assuming a fractionation rate of 2.54‰). The native scale eater *Roeboides* sp. was enriched by 0.99‰ in $\delta^{15}N$ in Gatun relative to Bayano ($W = 0$, $p = 0.002$), corresponding to an increase of approximately 0.4 trophic levels. In contrast, the omnivore *Brycon* sp. was significantly depleted in $\delta^{15}N$ in Gatun relative to Bayano ($t = 9.09$, $p < 0.001$), which corresponded to a drop in 1.5 trophic levels. For *Brycon* sp., this drop in TP was accompanied by an almost 10-fold reduction in the relative biomass of *Brycon* sp., from 40.8% of community biomass in Bayano to only 4.6% of biomass in Gatun (Figure 4).

DISCUSSION

To examine how invasion might alter food web structure, we characterized for the first time the food webs of two large Neotropical lakes that differ markedly in the level of invasion.

In what follows, we review the major structural differences between these two food webs and discuss the extent to which these differences may relate to biological invasion versus other ecological factors.

How does trophic structure differ between a heavily invaded versus minimally invaded assemblage?

We found that the fish community of the heavily invaded Lake Gatun exhibited a longer food chain and greater overall isotopic diversity relative to the minimally invaded Lake Bayano. This is consistent with findings from temperate freshwater systems, where increases in food chain length (Walsworth et al., 2013; Woodward &

Hildrew, 2001) and overall isotopic niche breadth (i.e., trophic dispersion; Rogosch & Olden, 2020; Wainright et al., 2021) have been reported following invasion. This increase in isotopic diversity may be partially driven by the greater richness of Lake Gatun, as the core isotopic niche (SEAc) has been shown to correlate positively with species richness globally (Sagouis et al., 2015). The longer food chain in Gatun was due in part to invasions by multiple novel apex predators (mostly of marine origin, e.g., *Centropomus* sp.), reminiscent of the "top-heavy" food webs that often characterize anthropogenically impacted lakes (Eby et al., 2006). However, the lengthening of the food chain in Gatun was also due to the introduction of novel herbivores at the bottom of the food web (e.g., *M. festivus*, *M. curema*). This is consistent with a meta-analysis by Sagouis et al. (2015), who found that, across 305 lentic ecosystems globally, the number of non-native primary consumers was positively associated with $\delta^{15}N$ range.

Body size distributions also differed markedly between the two lakes, with Lake Gatun occupying a greater length range relative to that occupied by the primarily native freshwater fish community of Lake Bayano. While this was primarily due to the addition of large-bodied non-native fishes (matching global patterns: Blanchet et al., 2010; Eby et al., 2006), it was also driven by the introduction of small-bodied insectivores like *G. holbrooki*. Body size is a key functional trait that is known to scale with a number of life history and ecological attributes (e.g., metabolic rate, ingestion rate, longevity, TP, numerical abundance, home range size), which in turn can influence ecosystem function (Woodward et al., 2005). Shifts in body size distribution can influence community structure and dynamics in a variety of ways, including by altering the prevalence of intraguild predation, the potential for stoichiometric imbalances, and the temporal and spatial scaling of food webs. Most importantly, shifts toward larger body sizes (as observed here) can increase the probability of disturbances being propagated through a food web and, thus, decrease stability (Woodward et al., 2005).

To what extent do native and non-native trophic guilds overlap in isotopic niche space?

Theory suggests that successful invasion and establishment are more likely if an invader differs from resident species in terms of traits and/or resource use (David et al., 2017; Olden et al., 2006). In the context of isotopic niches, this leads to the prediction that established non-native species should be found either completely outside, or at the margin of, the isotopic niche space defined by the resident community. This prediction was partially supported by our data from Lake Gatun, with patterns varying across trophic guilds. For carnivores, the mean isotopic positions of several non-native species were located outside, or on the periphery, of the isotopic niche space defined by native species. However, at the guild level, there was considerable overlap in the core isotopic niches (SEAc) of native and non-native carnivores. Notably, this overlap was asymmetrical, with native carnivores experiencing the highest degree of overlap, both from marine carnivores (81% overlap) and introduced carnivores (100% overlap). Substantial overlap in the isotopic niches of native and non-native species has also been observed in marine fishes in the Eastern Mediterranean (Fanelli et al., 2015) and in North American desert stream fishes (Rogosch & Olden, 2020; Walsworth et al., 2013).

The apparent coexistence of multiple native and non-native carnivores with highly overlapping isotopic niches has several possible explanations. First, it is possible for species to exhibit similar isotopic signatures but still have subtly different underlying diets, for example, if they consume different prey species, but these prey have similar isotopic signatures (Layman et al., 2012). Second, species may have similar diets but may partition resources along other unmeasured niche dimensions, for example, by feeding at different times of day or in different habitats. Third, unmeasured increases in the biomass at the base of the food web (e.g., due to eutrophication) may facilitate the coexistence of multiple higher consumers. Either way, the addition of so many non-native carnivores without any associated extirpations of native carnivores (Sharpe et al., 2017; Valverde et al., 2020) might suggest that the original food web of Gatun was not saturated. This echoes earlier findings from the same watershed, where biotic interchange following the completion of the Panama Canal led to increases in local species richness and no extirpations, suggesting local freshwater fish communities were not saturated (Smith et al., 2004). However, most of the non-native carnivores included in our food web have arrived within the last few decades (Gutiérrez et al., 1995; Sharpe et al., 2017; Zaret & Paine, 1973). The fact that many native carnivores and omnivores had substantially lower abundance and biomass in Lake Gatun relative to Lake Bayano (Sharpe et al., 2017; Valverde et al., 2020) suggests that they could be experiencing lower growth and reproduction rates due to competition with non-native carnivores, and their populations may decline over time. Therefore, it is possible that not enough time has yet elapsed for competitive exclusion to occur, and this apparent coexistence may be transitory. Alternatively, biotic resistance

due to negative interspecific interactions with native species might limit the establishment of some of these recently arrived species in the long-term.

In contrast to the pattern seen for carnivores in Gatun, three out of four non-native herbivores in Gatun had mean isotopic positions that were far outside of the native convex hull polygon, and we observed low (20%–29%) overlap in the core isotopic niches of native versus non-native herbivores. This low contemporary overlap may reflect niche shifts in native herbivores, something that is supported by comparing the contemporary isotopic position of *C. magdalenae* across lakes. In Lake Bayano, this species had a $\delta^{13}C$ signature that was intermediate between the pelagic and littoral baselines, suggesting a roughly equal integration of both source pools. However, in Lake Gatun, it was located directly above the pelagic baseline, suggesting a much stronger reliance on pelagic carbon sources like phytoplankton. This shift might indicate competitive displacement by introduced littoral herbivores (*M. festivus*, *C. rendalli*, and *M. curema*), although differences in basal resources across lakes could also play a role (see following discussion).

How do the trophic positions of native species differ across lakes?

Three native freshwater taxa exhibited shifts in isotopic position between the highly invaded (Gatun) versus minimally invaded (Bayano) context. First, the native omnivore *Brycon* sp. had a substantially lower TP and reduced biomass in Lake Gatun relative to Lake Bayano. We hypothesize that these shifts could be due to competition from multiple introduced piscivores in Gatun. In a concurrent study of the diet of this species, we found evidence for a shift from piscivory in Lake Bayano to insectivory in Lake Gatun (Sharpe et al., in preparation). Specifically, in Lake Bayano, *B. striatulus* fed primarily on terrestrial plants (56%) and fish (36%). In contrast, in Lake Gatun, its congener *Brycon chagrensis* fed mainly on aquatic insects (83%) and terrestrial plants (17%; Sharpe et al., in preparation). However, because we were limited to mensurative comparisons between two lakes, alternative hypotheses cannot be ruled out (see following discussion). In contrast, we observed an increase in TP (i.e., more enriched $\delta^{15}N$ signatures) in two native carnivores, *H. microlepis* and *Roeboides* sp., in Gatun relative to Bayano. This observation was somewhat unexpected, given that native predators have often been found to shift to feeding on lower trophic levels in association with the introduction of novel apex predators (Olowo & Chapman, 1999; Rogosch & Olden, 2020; Vander Zanden et al., 1999; Wainright et al., 2021). However, it may be explained by the particular feeding ecology of these two species. *H. microlepis* is typically a strict piscivore, but our previous work showed that it has broadened its trophic niche to include scavenging on fishery discards in Gatun, probably in response to increased availability of this resource coupled with competition for its natural fish prey with *C. monoculus* and other introduced piscivores (Valverde et al., 2020). *Roeboides* spp. are scale-eaters that feed by rapidly approaching live fishes (often much larger than themselves) and quickly tearing away scales and tissue (Breder, 1927; Bussing, 2002). The enriched $\delta^{15}N$ signature of *Roeboides* spp. in Gatun may reflect feeding on scales from several of the introduced piscivores now present in the lake, although this hypothesis awaits direct testing through examination of stomach contents.

Caveats and alternative hypotheses

Overall, we found significant differences in trophic structure between a heavily invaded (Gatun) versus minimally invaded (Bayano) lake. We hypothesize that fish invasions are likely the major driver of these differences, especially since the lakes are similar in many other key aspects (Appendix S1). However, as noted earlier, given the lack of replication and mensurative nature of our study, we cannot conclusively rule out alternative hypotheses, which we consider here. First, Lake Gatun experiences high levels of ship traffic through the Panama Canal. Noise pollution from shipping can influence fish movement patterns and foraging behavior (Popper & Hawkins, 2019) and, thus, could indirectly influence trophic structure. Second, parts of Lake Gatun are regularly dredged to maintain canal operations, which results in high levels of turbidity in some areas (Escobar-Camacho et al., 2019). Turbidity limits the range of wavelengths available to visual predators and, thus, can alter their functional responses to different prey and, ultimately, their diets (Huenemann et al., 2012). Dredging also affects the quality of the benthic habitat and the availability of benthic prey, which could have bottom-up effects on the food web. However, given the large geographic extent of our sampling and the fact that we did not sample near these localized disturbances, it seems unlikely that they strongly influenced our results. Third, more generally, the abundance and diversity of basal resources (e.g., detritus, phytoplankton, periphyton, macrophytes) could differ across lakes. While we were able to account for some of this variation by correcting the isotopic values of secondary consumers by lake-specific isotopic baselines, differences in the abundance of basal resources across lakes could still indirectly

drive additional variation in food web structure. Fourth, the abundance and diversity of terrestrial and avian apex consumers (e.g., crocodiles, piscivorous birds) were not quantified here but could vary across lakes. Future work incorporating both higher and lower trophic levels in the lake and surrounding riparian habitats would enhance our understanding of the whole-food-web consequences of fish invasions in Lake Gatun, including cascading effects on other trophic levels, as hypothesized by Zaret and Paine (1973). Fifth, there are artisanal fisheries in both lakes, primarily targeting Nile tilapia and Peacock bass (PREPAC, 2005, 2006). Temporal and spatial variation in fishing pressure both within and across lakes could affect the distribution and biomass of target species, with indirect effects on the food web.

Sixth, it is still unknown whether the recently arrived marine species have established permanent breeding populations in Lake Gatun or whether they move repeatedly in and out through the locks. In our study, all of the marine fish were collected from sites in Lake Gatun that were located between 25 and 34 km inland. Thus, it seems fairly improbable that the individuals we captured at these sites would be regularly migrating back and forth to the Atlantic Ocean (a round-trip distance of 50–70 km, which would include navigating three sets of locks in each direction). Furthermore, we quantified carbon and nitrogen ratios in dorsal muscle tissue, which has a turnover time of approximately 1–3 months in fish (Buchheister & Latour, 2010). Thus, even if some of these marine fishes had migrated into Lake Gatun as juveniles, it is most likely (given the distances reported above) that they were residents of the lake for at least several months prior to capture, that is, for the time scale relevant to our sampling. Finally, reservoir age is known to affect fish community composition and trophic structure (Agostinho et al., 1999). Lakes Gatun and Bayano differ in age (108 vs. 48 years, respectively); however, Neotropical reservoirs typically stabilize 5–10 years after impoundment (Agostinho et al., 1999), so this difference in age may not be consequential. Future research should focus on trying to disentangle the influence of invasion from these other potential drivers.

CONCLUSION

The global breakdown of biogeographic barriers, in concert with other forms of global change, is increasingly leading to the formation of novel, or "no-analog," ecosystems with high proportions of non-native species that bear little resemblance to historical assemblages (Hobbs et al., 2009). These mixed assemblages provide fascinating opportunities to observe how novel food webs are assembled when multiple species with little or no coevolutionary history begin interacting with one another. Past work in invaded temperate freshwater systems suggests that food webs in mixed assemblages are structurally different, and usually isotopically more diverse, than the original food webs they replaced (Rogosch & Olden, 2020; Wainright et al., 2021; Woodward & Hildrew, 2001). Our work extends these findings to tropical systems, which generally have fewer established invasive species relative to comparable ecosystems at higher latitudes (Sax, 2001). One hypothesis for this pattern is that stronger interspecific interactions in the tropics limit the establishment of non-native species, essentially providing a form of "biotic resistance" to invasion (Elton, 1958). Indeed, recent experimental evidence indicates that predation on non-native species—a key form of biotic resistance—is three times greater in marine epifaunal communities in Panama relative to the temperate zone (Freestone et al., 2013). Interestingly, our work suggests that even a highly diverse tropical lake like Gatun can accommodate (in the short term at least) multiple non-native species that show strong trophic overlap with native species. Future work should focus on quantifying the proportion of these species that becomes permanently established in the lake and how the structure and dynamics of the food web might continue to change over the coming decades. This will be particularly important given that the influx of marine and estuarine species into Lake Gatun appears to have accelerated in recent years, likely as a result of the recently completed expansion of the Panama Canal (Castellanos-Galindo et al., 2020; Schreiber et al., 2023).

ACKNOWLEDGMENTS

We gratefully acknowledge L. Aponte, V. Bravo, M. Deveaine, V. Frankel, I. Geladi, R. González, C. Martínez, L. Ortíz, J. L. Pereira, K. Roberts, R. Ryan, C. Schloeder, and S. VanDoren for valuable field and lab assistance. We thank the fishing communities of Cuipo, Gamboa, and Nicora, especially F. Martínez and family and N. Espino, for their hospitality and assistance. The staff of STRI's Naos Laboratories and Barro Colorado Island Field Station and INDICASAT provided invaluable logistical support. R. Cooke, R. González, R. Robertson, and C. Vergara helped identify specimens. We thank Panama's Autoridad del Canal (ACP) and Ministerio del Ambiente for permission to collect fish as part of this study (Permit nos. SE/AP-21-13, SC/A-29-13, SE/AP-11-15, SE/AP-40-15). Funding was provided by Natural Sciences and Engineering Research Council of Canada (NSERC) (NSERC CREATE in Biodiversity Ecosystem Services and Sustainability, BESS), STRI, the National Geographic Society (Grant no. 3221-4),

SENACYT (Grant no. ITE12-002 to Luis F. De León), and the Sistema Nacional de Investigadores de Panama (to Diana M. T. Sharpe and Luis F. De León). We thank two anonymous reviewers and the editorial team at *Ecology* for constructive comments that helped improve the manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Sharpe, 2023) are available in Figshare at https://doi.org/10.6084/m9.figshare.21429201.

ORCID

Diana M. T. Sharpe https://orcid.org/0000-0002-3986-4725
Andrew P. Hendry https://orcid.org/0000-0002-4807-6667
Mark E. Torchin https://orcid.org/0000-0002-0103-577X

REFERENCES

Agostinho, A. A., L. E. Miranda, L. M. Bini, L. C. Gomes, S. M. Thomaz, and H. I. Suzuki. 1999. "Patterns of Colonization in Neotropical Reservoirs, and Prognoses on Aging." In *Theoretical Reservoir Ecology and Applications,* edited by J. G. Tundisi and M. Straskraba, 227–265. Leiden, Netherlands: Backhuys.

Albert, J. S., V. A. Tagliacollo, and F. Dagosta. 2020. "Diversification of Neotropical Freshwater Fishes." *Annual Review of Ecology, Evolution, and Systematics* 51: 27–53.

Amundsen, P. A., K. D. Lafferty, R. Knudsen, R. Primicerio, R. Kristoffersen, A. Klemetsen, and A. M. Kuris. 2013. "New Parasites and Predators Follow the Introduction of Two Fish Species to a Subarctic Lake: Implications for Food-Web Structure and Functioning." *Oecologia* 171: 993–1002.

Bearhop, S., C. E. Adams, S. Waldron, R. A. Fuller, H. Macleod, R. A. Fullert, and H. Macleodj. 2004. "Determining Trophic Niche Width: A Novel Approach Using Stable Isotope Analysis." *Journal of Animal Ecology* 73: 1007–12.

Blanchet, S., G. Grenouillet, O. Beauchard, P. A. Tedesco, F. Leprieur, H. H. Dürr, F. Busson, T. Oberdorff, and S. Brosse. 2010. "Non-native Species Disrupt the Worldwide Patterns of Freshwater Fish Body Size: Implications for Bergmann's Rule." *Ecology Letters* 13: 421–431.

Breder, C. 1927. "The Fishes of the Rio Chucunaque Drainage, Eastern Panama." *Bulletin of the American Museum of Natural History* 57: 91–176.

Breder, C. 1944. "A Revised List of the Fishes of Barro Colorado, Gatún Lake, Panama." *Copeia* 1944: 86–89.

Britton, J. R., G. D. Davies, and C. Harrod. 2010. "Trophic Interactions and Consequent Impacts of the Invasive Fish Pseudorasbora Parva in a Native Aquatic Foodweb: A Field Investigation in the UK." *Biological Invasions* 12: 1533–42.

Buchheister, A., and R. J. Latour. 2010. "Turnover and Fractionation of Carbon and Nitrogen Stable Isotopes in Tissues of a Migratory Coastal Predator, Summer Flounder (*Paralichthys dentatus*)." *Canadian Journal of Fisheries and Aquatic Sciences* 67: 445–461.

Bussing, W. A. 2002. *Freshwater Fishes of Costa Rica*. San Jose: Universidad de Costa Rica.

Cabana, G., and J. B. Rasmussen. 1996. "Comparison of Aquatic Food Chains Using Nitrogen Isotopes." *Proceedings of the National Academy of Sciences* 93: 10844–47.

Castellanos-Galindo, G. A., D. R. Robertson, D. M. T. Sharpe, and M. E. Torchin. 2020. "A New Wave of Marine Fish Invasions through the Panama and Suez Canals." *Nature Ecology and Evolution* 4: 1444–46.

Cohen, A. N. 2006. "Species Introductions and the Panama Canal." In *Bridging Divides,* edited by A. N. Cohen, S. Gollasch and B. S. Galil, 127–206. Dordrecht: Springer.

Cucherousset, J., S. Bouletreau, A. Martino, J.-M. Roussel, and F. Santoul. 2012. "Using Stable Isotope Analyses to Determine the Ecological Effects of Non-native Fishes." *Fisheries Management and Ecology* 19: 111–19.

David, P., E. Thébault, O. Anneville, P. F. Duyck, E. Chapuis, and N. Loeuille. 2017. "Impacts of Invasive Species on Food Webs: A Review of Empirical Data." *Advances in Ecological Research* 56: 1–60.

Eby, L. A., W. J. Roach, L. B. Crowder, and J. A. Stanford. 2006. "Effects of Stocking-up Freshwater Food Webs." *Trends in Ecology & Evolution* 21: 576–584.

Elton, C. S. 1958. *The Ecology of Invasions by Plants and Animals*. Methuen: Springer.

Escobar-Camacho, D., M. E. R. Pierotti, V. Ferenc, D. M. T. Sharpe, E. Ramos, C. Martins, and K. L. Carleton. 2019. "Variable Vision in Variable Environments: The Visual System of an Invasive Cichlid (*Cichla monoculus*) in Lake Gatun, Panama." *Journal of Experimental Biology* 222: 188300.

Fanelli, E., E. Azzurro, M. Bariche, J. E. Cartes, and F. Maynou. 2015. "Depicting the Novel Eastern Mediterranean Food Web: A Stable Isotopes Study Following Lessepsian Fish Invasion." *Biological Invasions* 17: 2163–78.

Freestone, A. L., G. M. Ruiz, and M. E. Torchin. 2013. "Stronger Biotic Resistance in Tropics Relative to Temperate Zone: Effects of Predation on Marine Invasion Dynamics." *Ecology* 94: 1370–77.

Fry, B. 2006. *Stable Isotope Ecology*. New York: Springer.

Gonzalez, R. 1995. "Estado de los Peces Exoticos Introducidos en las Aguas Continentales de Panama." *Brenesia* 43–44: 55–59.

Guiterrez, R., R. Amores, R. Gonzalez, E. Areia, R. Bravo, and R. Yansic. 1995. "El inventario biologico del canal de Panama. IV. El estudio de aguas continentales y entomologico." *Scientia* 4: 17–81.

Gutiérrez, R., R. Amores, R. González, E. Area, R. Bravo, R. Yansic, E. Arcia, R. Bravo, and R. Yansic. 1995. "Inventario biológico del canal de Panamá: estudio de aguas continentales." *Scientia* 4: 17–81.

Hildebrand, S. F. 1939. "The Panama Canal as a Passageway for Fishes, with Lists and Remarks on the Fishes and Invertebrates." *Zoologica* 24: 15–45.

Hobbs, R. J., E. Higgs, and J. A. Harris. 2009. "Novel Ecosystems: Implications for Conservation and Restoration." *Trends in Ecology and Evolution* 24: 599–605.

Huenemann, T. W., E. D. Dibble, and J. P. Fleming. 2012. "Influence of Turbidity on the Foraging of Largemouth Bass." *Transactions of the American Fisheries Society* 141: 107–111.

Jackson, A. L., R. Inger, A. C. Parnell, and S. Bearhop. 2011. "Comparing Isotopic Niche Widths among and within Communities: SIBER-Stable Isotope Bayesian Ellipses in R." *Journal of Animal Ecology* 80: 595–602.

Jackson, M. C., R. J. Wasserman, J. Grey, A. Ricciardi, J. T. A. Dick, and M. E. Alexander. 2017. "Novel and Disrupted Trophic Links Following Invasion in Freshwater Ecosystems." *Advances in Ecological Research* 57: 55–97.

Jepsen, D. B., and K. O. Winemiller. 2002. "Structure of Tropical River Food Webs Revealed by Stable Isotope Ratios." *Oikos* 96: 46–55.

Layman, C. A., M. S. Araujo, R. Boucek, C. M. Hammerschlag-Peyer, E. Harrison, Z. R. Jud, P. Matich, et al. 2012. "Applying Stable Isotopes to Examine Food-Web Structure: An Overview of Analytical Tools." *Biological Reviews* 87: 545–562.

Layman, C. A., M. S. Program, N. Miami, L. R. District, E. Biology, and N. Haven. 2007. "Can Stable Isotope Ratios Provide for Community-Wide Measures of Trophic Structure?" *Ecology* 88: 42–48.

Layman, C. A., J. P. Quattrochi, C. M. Peyer, and J. E. Allgeier. 2007. "Niche Width Collapse in a Resilient Top Predator Following Ecosystem Fragmentation." *Ecology Letters* 10: 937–944.

Layman, C. A., K. O. Winemiller, and D. A. Arrington. 2005. "Describing a Species-Rich River Food Web Using Stable Isotopes, Stomach Contents, and Functional Experiments." In *Dynamic Food Webs: Multispecies Assemblages, Ecosystem Development and Environmental Change*, edited by J. C. M. P. C. de Ruiter and V. Wolters, 395–406. Amsterdam: Elsevier.

Lévêque, C., T. Oberdorff, D. Paugy, M. L. J. Stiassny, and P. A. Tedesco. 2008. "Global Diversity of Fish (Pisces) in Freshwater." *Hydrobiologia* 595: 545–567.

Meek, S. E., and S. F. Hildebrand. 1916. *The Fishes of the Freshwaters of Panama*. Chicago: Field Museum of Natural History.

Newsome, S. D. S. D., C. Martínez Del Rio, S. Bearhop, and D. L. Phillips. 2007. "A Niche for Isotopic Ecology." *Frontiers in Ecology and the Environment* 5: 429–436.

Olden, J. D., N. L. Poff, and K. R. Bestgen. 2006. "Life-History Strategies Predict Fish Invasions and Extirpations in the Colorado River Basin." *Ecological Monographs* 76: 25–40.

Olowo, J. P., and L. J. Chapman. 1999. "Trophic Shifts in Predatory Catfishes Following the Introduction of Nile Perch into Lake Victoria." *African Journal of Ecology* 37: 457–470.

Ozersky, T., D. O. Evans, and D. R. Barton. 2012. "Invasive Mussels Alter the Littoral Food Web of a Large Lake: Stable Isotopes Reveal Drastic Shifts in Sources and Flow of Energy." *PLoS One* 7: e51249.

Peterson, B. J., and B. Fry. 1987. "Stable Isotopes in Ecosystem Studies." *Annual Review of Ecology and Systematics* 18: 293–320.

Polis, G. A., and K. O. Winemiller. 2013. *Food Webs: Integration of Patterns and Dynamics*. Berlin: Springer Science & Business Media.

Popper, A. N., and A. D. Hawkins. 2019. "An Overview of Fish Bioacoustics and the Impacts of Anthropogenic Sounds on Fishes." *Journal of Fish Biology* 94: 692–713.

Post, D. M. 2002. "Using Stable Isotopes to Estimate Trophic Position: Models, Methods, and Assumptions." *Ecology* 83: 703–718.

PREPAC. 2005. *Inventario de cuerpos de agua continentales de la República de Panamá con énfasis en la pesca y la acuicultura*. San Salvador, El Salvador: Sistema de la Integracion Centroamericaan (SICA). 66 pp. Available at: https://www.sica.int/download/?9932.

PREPAC. 2006. *Caracterizacion del lago Bayano con enfasis en la pesca y la acuicultura*. San Salvador, El Salvador: Sistema de la Integracion Centroamericaan (SICA). 102 pp.

Rogosch, J. S., and J. D. Olden. 2020. "Invaders Induce Coordinated Isotopic Niche Shifts in Native Fish Species." *Canadian Journal of Fisheries and Aquatic Sciences* 77: 1348–58.

Sagouis, A., J. Cucherousset, S. Villéger, F. Santoul, and S. Boulêtreau. 2015. "Non-native Species Modify the Isotopic Structure of Freshwater Fish Communities across the Globe." *Ecography* 38: 979–985.

Sax, D. F. 2001. "Latitudinal Gradients and Geographic Ranges of Exotic Species: Implications for Biogeography." *Journal of Biogeography* 28: 139–150.

Schreiber, L., G. A. Castellanos-Galindo, D. R. Robertson, M. Torchin, K. Chavarria, S. Laakmann, and K. Saltonstall. 2023. "Environmental DNA (eDNA) Reveals Potential for Interoceanic Fish Invasions across the Panama Canal." *Ecology and Evolution* 13: e9675.

Sharpe, D. 2023. "Sharpe_Raw Gatun SIA Data.csv." Figshare, Dataset. https://doi.org/10.6084/m9.figshare.21429201.v1.

Sharpe, D. M. T., L. F. De León, R. González, and M. E. Torchin. 2017. "Tropical Fish Community Does Not Recover 45 Years after Predator Introduction." *Ecology* 98: 412–424.

Sharpe, D. M. T., M. P. Valderde, V. Bravo, R. Gonzalez, and L. F. De Leon. in preparation. "Exploring the Trophic Ecology of Native and Introduced Freshwater Fishesin Panama."

Smith, S. A., G. Bell, and E. Bermingham. 2004. "Cross-Cordillera Exchange Mediated by the Panama Canal Increased the Species Richness of Local Freshwater Fish Assemblages." *Proceedings of the Royal Society B: Biological Sciences* 271: 1889–96.

Smith, S. A., and E. Bermingham. 2005. "The Biogeography of Lower Mesoamerican Freshwater Fishes." *Journal of Biogeography* 32: 1835–54.

Toussaint, A., N. Charpin, S. Brosse, and S. Villéger. 2016. "Global Functional Diversity of Freshwater Fish Is Concentrated in the Neotropics while Functional Vulnerability Is Widespread." *Scientific Reports* 6: 1–9.

Valverde, M. P., D. M. T. Sharpe, M. E. Torchin, D. G. Buck, and L. J. Chapman. 2020. "Trophic Shifts in a Native Predator Following the Introduction of a Top Predator in a Tropical Lake." *Biological Invasions* 22: 643–661.

Vander Zanden, M. J., J. M. Casselman, and J. B. Rasmussen. 1999. "Stable Isotope Evidence for the Food Web Consequences of Species Invasions in Lakes." *Nature* 401: 464–67.

Vanderklift, M. A., and S. Ponsard. 2003. "Sources of Variation in Consumer-Diet δ15N Enrichment: A Meta-Analysis." *Oecologia* 136: 169–182.

Wainright, C. A., C. C. Muhlfeld, J. J. Elser, S. L. Bourret, and S. P. Devlin. 2021. "Species Invasion Progressively Disrupts the

Trophic Structure of Native Food Webs." *Proceedings of the National Academy of Sciences* 118: 1–5.

Walsworth, T. E., P. Budy, and G. P. Thiede. 2013. "Longer Food Chains and Crowded Niche Space: Effects of Multiple Invaders on Desert Stream Food Web Structure." *Ecology of Freshwater Fish* 22: 439–452.

Woodward, G., B. Ebenman, M. Emmerson, J. M. Montoya, J. M. Olesen, A. Valido, and P. H. Warren. 2005. "Body Size in Ecological Networks." *Trends in Ecology and Evolution* 20: 402–9.

Woodward, G., and A. G. Hildrew. 2001. "Invasion of a Stream Food Web by a New Top Predator." *Journal of Animal Ecology* 70: 273–288.

Zaret, T. M., and R. T. Paine. 1973. "Species Introduction in a Tropical Lake." *Science* 182: 449–455.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Sharpe, Diana M. T., Marisol P. Valverde, Luis F. De León, Andrew P. Hendry, and Mark E. Torchin. 2023. "Biological Invasions Alter the Structure of a Tropical Freshwater Food Web." *Ecology* e4173. https://doi.org/10.1002/ecy.4173