



# Species invasion progressively disrupts the trophic structure of native food webs

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Contributed by James J. Elser, June 15, 2021 (sent for review February 8, 2021; reviewed by Wyatt F. Cross and M. Jake Vander Zanden)

**Species invasions can have substantial impacts on native species and ecosystems, with important consequences for biodiversity. How these disturbances drive changes in the trophic structure of native food webs through time is poorly understood. Here, we quantify trophic disruption in freshwater food webs to invasion by an apex fish predator, lake trout, using an extensive stable isotope dataset across a natural gradient of uninhabited and invaded lakes in the northern Rocky Mountains, USA. Lake trout invasion increased fish diet variability (trophic dispersion), displaced native fishes from their reference diets (trophic displacement), and reorganized macroinvertebrate communities, indicating strong food web disruption. Trophic dispersion was greatest 25 to 50 y after colonization and dissipated as food webs stabilized in later stages of invasion (>50 y). For the native apex predator, bull trout, trophic dispersion preceded trophic displacement, leading to their functional loss in late-invasion food webs. Our results demonstrate how invasive species progressively disrupt native food webs via trophic dispersion and displacement, ultimately yielding biological communities strongly divergent from those in uninhabited ecosystems.**

food web | invasive species | stable isotope | lake trout | bull trout

Invasive species have caused devastating ecological and economic impacts worldwide (1, 2). For example, invasive species are responsible for the decline of nearly half of the species protected by the US Endangered Species Act and those named on the International Union for Conservation of Nature Red List and cause almost US\$120 billion in annual damages in the United States alone (3, 4). The scope of these damages has prompted recent efforts to predict the vulnerability of ecosystems to species invasions and prioritize them for management (5, 6), a process contingent on our ability to understand the mechanisms by which invaders alter food webs through time (7). While the economic harm caused by invasive species is apparent, predicting trophic responses to species invasions remains challenging because complex ecological changes can compound through time (8, 9).

Species invasions change interactions within and between communities, with potentially severe consequences for biodiversity and ecosystems (10). Animals adapted to eat diverse foods (i.e., diet generalists) often change their diets to overcome increasing competition for food and/or to avoid new predators following species invasions (11). Those diet changes then manifest in the trophic structure of food webs in two main ways: changing diet variability [i.e., trophic dispersion (12), such as switching from a specialist to a generalist diet] or prey switching [i.e., trophic displacement (13), such as eating insects instead of fish]. Given these patterns, we propose the “trophic disruption hypothesis”: Species cause trophic dispersion and trophic displacement, which, given time, change food web structure and affect biodiversity. Despite some preliminary evidence that these trophic disruptions change as invasion progresses (14, 15), quantitative tests of this hypothesis across a range of intact and invaded ecosystems do not exist.

To test the trophic disruption hypothesis, we examined the trophic effects of an invasive piscivorous fish (lake trout; *Salvelinus namaycush*) across lake food webs in the northern Rocky Mountains, USA. Invasive predatory fishes provide an ideal system to test this hypothesis because they have been widely introduced across the globe and their ability to mediate major changes in the trophic structure of aquatic ecosystems is widely recognized (14). Lake trout have been intentionally, illegally, or invasively established in over 200 waters in western North America (16), resulting in cascading changes within and across ecosystems (17, 18). Populations of bull trout (*Salvelinus confluentus*), one of the most threatened cold-water fishes in North America, have dramatically declined in most lakes where lake trout have been introduced or invaded (16). Bull trout and lake trout are apex predators and share similar feeding strategies, diets, and morphologies, making competition and predation likely between these species (19). Despite this major conservation threat, no studies have evaluated the impacts of lake trout invasion across entire food webs supporting native bull trout.

We leveraged a natural experiment to quantify how trophic dispersion and displacement unfold following species invasion. Though otherwise comparable, our 10 study lakes that contained native bull trout populations ranged in invasion severity from reference (i.e., uninhabited) to fully dominated by lake trout. We used this invasion gradient to simulate the progression of trophic disruption over decades by classifying lakes on a scale of 0 to 1 based on the relative abundance of bull trout

## Significance

**Invasive species are a leading cause of biodiversity loss, yet the mechanisms by which invaders progressively disrupt ecosystems and native species remain unclear. Using an extensive isotope dataset across multiple ecosystems and stages of invasion, we show that an invasive fish predator (lake trout) disrupted food webs by forcing native fishes to feed on suboptimal food sources in different habitats, resulting in the functional extirpation of the native predator, threatened bull trout. Our results provide insights into the magnitude, direction, and timing of food web disruption from invasive species and will be important for predicting ecosystem consequences of species invasions.**

Author contributions: C.A.W., C.C.M., J.J.E., and S.P.D. designed research; C.A.W., C.C.M., and S.L.B. performed research; C.A.W., C.C.M., J.J.E., and S.P.D. analyzed data; and C.A.W., C.C.M., J.J.E., S.L.B., and S.P.D. wrote the paper.

Reviewers: W.F.C., Montana State University; and M.J.V.Z., University of Wisconsin–Madison.

The authors declare no competing interest.

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This article contains supporting information online at <http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2102179118/-DCSupplemental>.

Published November 1, 2021.

to lake trout (reference, 0; midinvasion, 0.4 to 0.8; and late invasion, 0.8 to 1). We used stable nitrogen (N) and carbon (C) isotopes (1,459 samples) to determine how fish diets changed as lake trout invasion progressed. Stable isotope analyses provide time-integrated and energy-based depictions of trophic structure that facilitate understanding food web consequences of species invasions (13). The ratio of stable nitrogen isotopes ( $^{15}\text{N}:$  $^{14}\text{N}$ ;  $\delta^{15}\text{N}$ ) exhibits stepwise enrichment (often 3 to 4‰) between prey and predators and is used to infer the trophic position of consumers (20). The ratio of stable carbon isotopes ( $^{13}\text{C}:$  $^{12}\text{C}$ ;  $\delta^{13}\text{C}$ ) varies substantially (>10‰) between littoral-benthic and pelagic primary producers but changes little (often <1‰) from prey to predators and is used to infer energy sources used for secondary production (20). By combining long-term abundance monitoring data and stable isotope analyses, we determined how invasion-induced trophic dispersion and displacement changed over time in these lake food webs.

## Results

Lake trout invasion restructured food webs and produced substantial trophic dispersion (i.e., diet variability) in four of five fish groups (Figs. 1 and 24). Trophic dispersion, indicated by isotope ellipse area, was low in reference lakes, increased in midinvasion lakes, and declined in late-invasion lakes for bull trout and generalist fishes, but increased and remained elevated for lake trout and littoral forage fish. Unlike other fish groups, pelagic fish isotope ellipse areas did not differ across invasion states. Overall, these results show that the magnitude of trophic dispersion from lake trout invasion was greatest in midinvasion lakes.

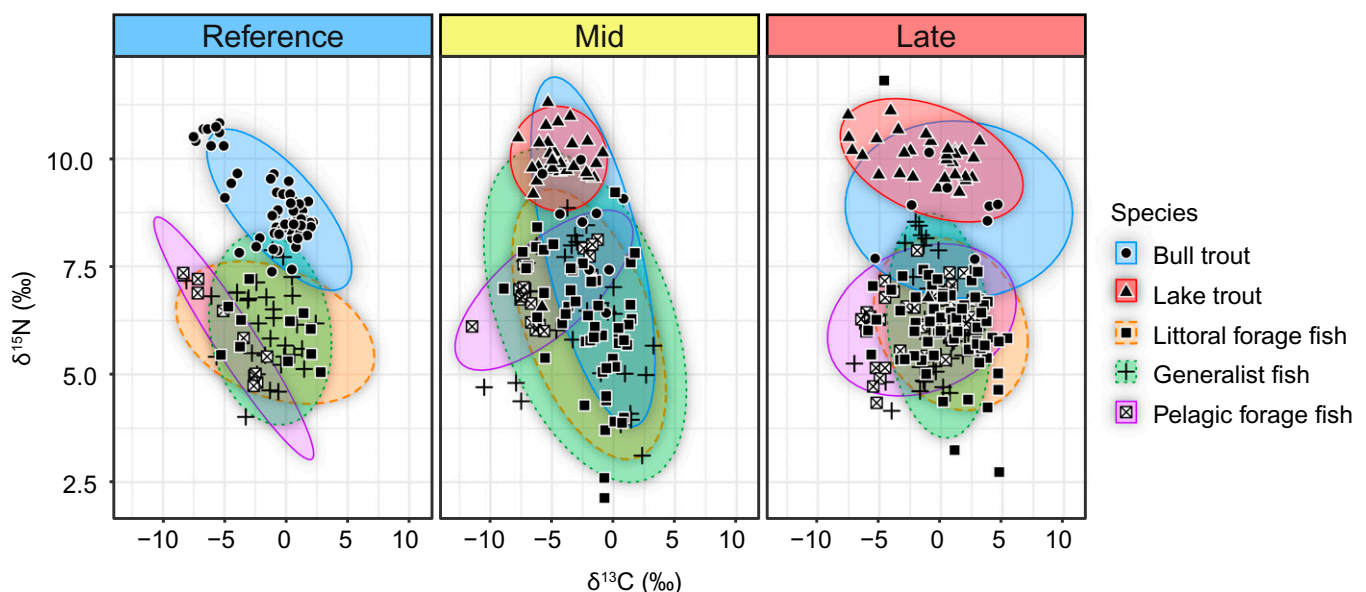
$\delta^{15}\text{N}$  trophic displacement of bull trout and pelagic forage fish increased with lake trout invasion, but the effect appeared to be temporary. Our study lakes had two fish trophic levels: piscivorous lake trout and bull trout with high  $\delta^{15}\text{N}$  and mesopredators with lower  $\delta^{15}\text{N}$  (Fig. 2B). Lake trout, generalist fish, and littoral forage fish maintained constant  $\delta^{15}\text{N}$  throughout invasion (Fig. 2B). In contrast, bull trout and pelagic forage fish  $\delta^{15}\text{N}$  shifted in opposite directions midinvasion (Fig. 2B and *SI Appendix, Table S1*). This  $\delta^{15}\text{N}$  inflection brought bull trout to within the 95% CIs of the mesopredator fish trophic position

(Figs. 1 and 2B and *SI Appendix, Table S1*), suggesting that bull trout functioned as mesopredators in midinvasion lakes. The increase of pelagic forage fish  $\delta^{15}\text{N}$  could reflect a changing zooplankton community from tritrophic interactions (21). By late invasion, bull trout and pelagic forage fish  $\delta^{15}\text{N}$  returned to reference levels, consistent with the dynamics of trophic dispersion for bull trout (Fig. 2B). Finally, lake trout  $\delta^{15}\text{N}$  was consistently higher than bull trout  $\delta^{15}\text{N}$  (mean differences: mid, 2.06‰; late, 1.02‰; Fig. 2B and *SI Appendix, Table S1*), suggesting that lake trout consumed bull trout; diet modeling was consistent with this interpretation, estimating that lake trout diet consisted of ~14% bull trout (*SI Appendix, Fig. S1*).

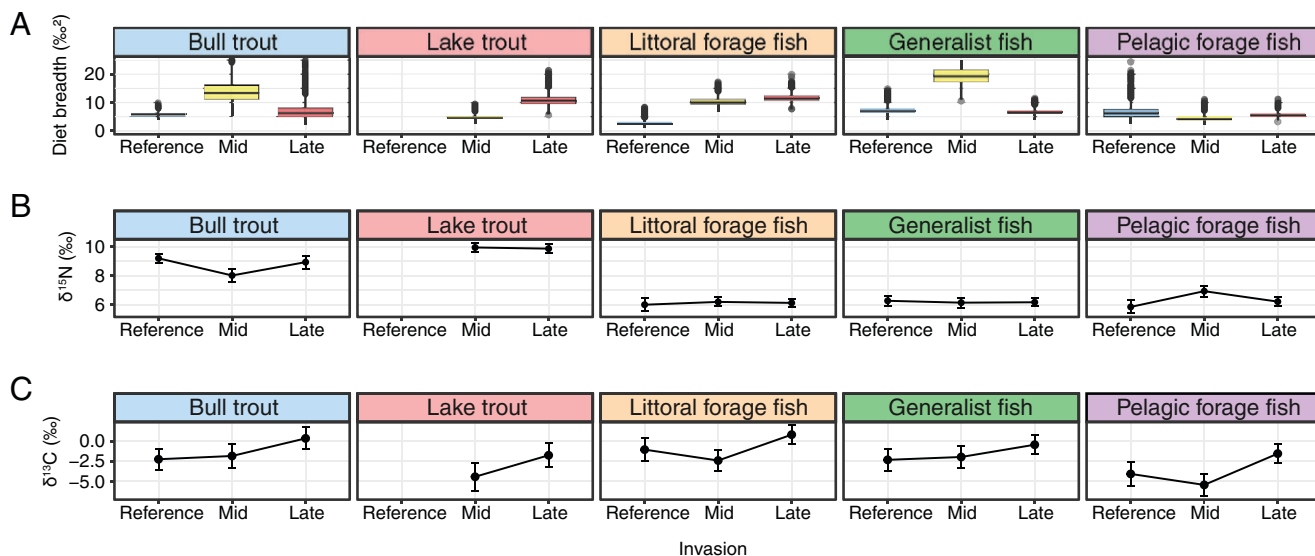
$\delta^{13}\text{C}$  trophic displacement increased for all fish species (Fig. 2C), either consistently across lake invasion status or as a discontinuous inflection. Bull trout and generalist fish  $\delta^{13}\text{C}$  increased throughout invasion, suggesting increased reliance on littoral prey as invasion progressed. Pelagic and littoral forage fish  $\delta^{13}\text{C}$  first declined and then increased, with small  $\delta^{13}\text{C}$  decreases from reference to midinvasion followed by larger  $\delta^{13}\text{C}$  increases from midinvasion and late invasion. Interestingly, lake trout  $\delta^{13}\text{C}$  also increased from mid- to late invasion, which may indicate decreasing abundances of pelagic forage fish and a subsequent shift to littoral prey (22).

Trophic structure ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) of littoral macroinvertebrates did not correlate with lake trout invasion status but littoral macroinvertebrate community structure did (permANOVA;  $F_{2,62} = 6.3$ ,  $P = 0.001$ ). Reference and midinvasion littoral macroinvertebrate communities were similar to one another in diversity and taxonomic identity (*SI Appendix, Fig. S2*). In contrast, late-invasion macroinvertebrate communities were widely dispersed in ordination space, indicating high beta diversity compared with reference or midinvasion communities and demonstrating that late-invasion communities differed from one another taxonomically and/or in diversity. Finally, 17 of 35 (49%) late-invasion macroinvertebrate communities fell outside the 95% CI ellipses of the reference or midinvasion communities, indicating that macroinvertebrate communities diverged as lake trout invasion progressed.

The isotopic signatures of bull trout and lake trout revealed asymmetric shifts in diet overlap between these apex predators as invasion progressed (Fig. 3A and B). Midinvasion bull trout



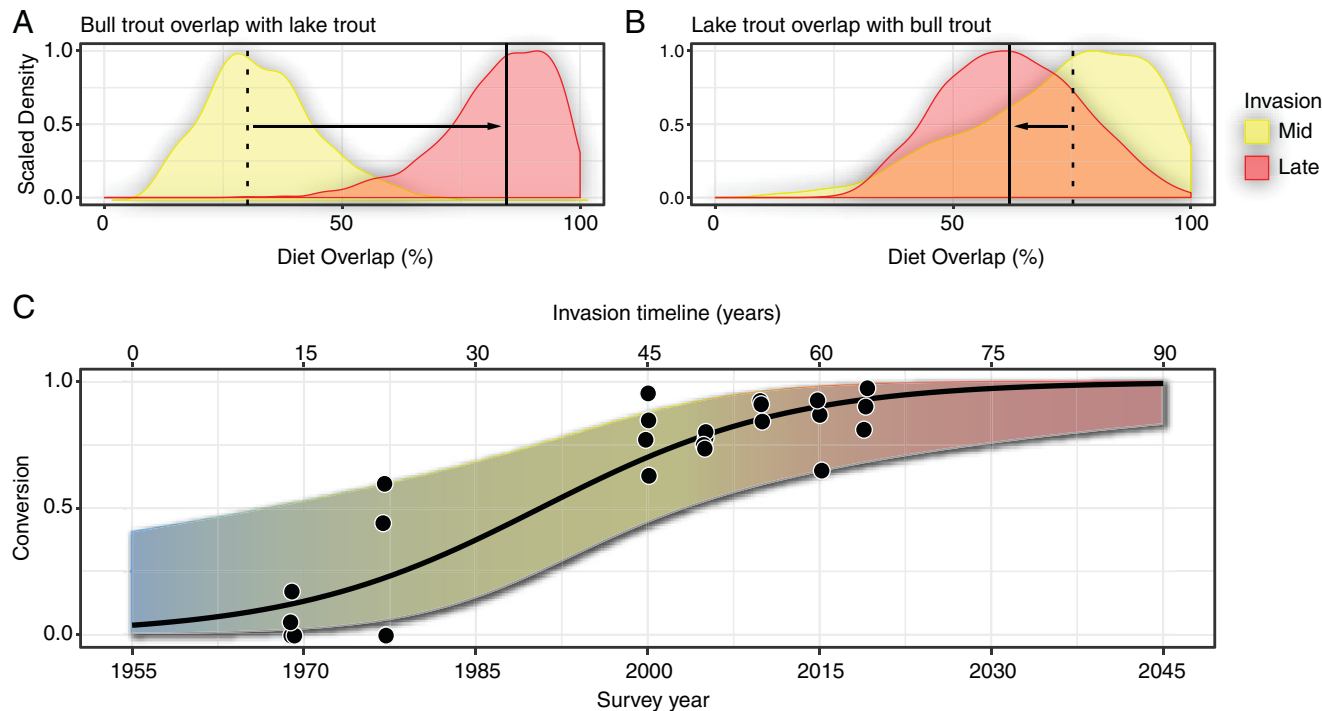
**Fig. 1.** Food web structure of uninvaded and invaded lakes. Baseline-corrected  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  for fish (points;  $n = 437$ ; *SI Appendix, Table S1*) from lakes representing reference, middle (Mid), and late stages of lake trout invasion (*SI Appendix, Table S2*). Mesopredator fish species were aggregated to functional groups (*SI Appendix, Table S3*). Ellipses are 95% CIs around mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  for each fish species or functional group.



**Fig. 2.** Stable isotope evidence for trophic dispersion and displacement. (A) Fish diet breadth, as indicated by posterior estimates of standard Bayesian ellipse areas, among phases of lake trout invasion (reference, mid-, and late invasion). Boxplots show median and interquartile range (boxes), minimum and maximum (whiskers), and outliers (points).  $n = 4,000$  posterior estimates.  $N_{fish}$  is provided in *SI Appendix, Table S1*. (B and C) Results from linear mixed-effects models comparing fish  $\delta^{15}N$  (B) and  $\delta^{13}C$  (C) to show directional changes in fish diet among phases of lake trout invasion. Model results are shown as mean  $\pm$  SE (points  $\pm$  error bars).  $P$  values are provided in *SI Appendix, Table S1*.

were displaced from their reference trophic position (Fig. 2B) and only shared 30% of the same diet as lake trout (50% credible interval; Fig. 3A, Mid and *SI Appendix, Table S4*). By late invasion, bull trout shared 85% of the same diet as lake trout

(50% credible interval; Fig. 3A, Late). In contrast, lake trout diet overlapped bull trout diet throughout the invasion (50% credible intervals: midinvasion, 62%; late invasion, 75%; Fig. 3B and *SI Appendix, Table S4*). These asymmetrical diet shifts



**Fig. 3.** Temporal dynamics of bull trout and lake trout diet overlap and lake conversion to lake trout dominance. (A and B) Scaled density histograms showing proportional diet overlap between bull trout and lake trout. (A) Proportion of bull trout diet overlapping lake trout diet. (B) Proportion of lake trout diet overlapping bull trout diet. Dotted and solid vertical lines are 50% credible intervals for proportional isotope ellipse overlap in midinvasion (yellow) and late-invasion (red) lakes, respectively. Summary statistics are provided in *SI Appendix, Table S4*. (C) Binomial linear regression of conversion through time in Logging, McDonald, Bowman, and Kintla lakes in Glacier National Park, Montana, USA. Data are presented as empirical conversion ( $n = 25$ ; black points) and predicted conversion (black curve;  $r^2 = 0.81$ ) with 95% CIs (blue-yellow-red ribbon). Binomial regression coefficients for invasion timeline (*SI Appendix, Table S5, Eq. 2*):  $\beta_0 = -3.251$  and  $\beta = 0.091$ . Empirical conversion data are from 1969 to 2019 standardized gill net surveys conducted by the US National Park Service (Glacier National Park). The invasion timeline converts the survey year of empirical data to years since predicted lake trout colonization (conversion,  $\sim 0$ ) in the study system.



reflect changing trophic dispersion and displacement among these species (Fig. 2) and suggest that lake trout competitively excluded bull trout from pelagic prey in midinvasion lakes but continued to compete with bull trout for food even as bull trout transitioned to littoral prey.

Using 50 y of long-term monitoring data collected in several of our study lakes, we developed a lake trout “conversion” metric (e.g., ref. 7; *SI Appendix*, Table S5, Eqs. 1–4) to estimate the chronology of bull trout displacement by tracking the relative abundance of lake trout to bull trout over time. Conversion values across invaded lakes showed that lake trout steadily displaced bull trout over time, resulting in complete dominance and functional extirpation of native bull trout ~85 y following lake trout colonization. Our conversion model suggests that lake trout were present for about 15 y prior to being detected, suggesting a considerable lag in the ability to detect lake trout in the early stages of invasion and colonization. These findings are consistent with other studies that have found that invaders can remain undetected for years following colonization in novel ecosystems (23).

## Discussion

The ecological consequences of species invasions are often assessed by comparing food webs before and after invasion in one or a few systems. In this study, we quantified invasion-induced food web disruption across a complete gradient of uninvaded and invaded lakes and found that trophic dispersion and displacement reverberated through food webs over decades. Across all fish species, the magnitude of trophic dispersion was generally greatest 25 to 50 y after colonization and dissipated as food webs stabilized in later stages of invasion. Trophic disruption was especially intense for the native top predator, bull trout, which were ultimately replaced by the invasive predator, lake trout, in late-invasion lakes. Together, our results demonstrate how invasive species initiate and maintain disruption of native food webs via trophic dispersion and trophic displacement, ultimately yielding divergent biological communities.

This study provides empirical evidence that species invasion destabilizes food webs through a stepwise series of trophic disruptions, resulting in a new ecological regime dominated by the invasive predator (24). First, stable trophic positions of predators and prey are one component of stable food webs (25) while trophic dispersion implicitly involves variability in trophic position (13). Lake trout invasion induced significant trophic dispersion, thereby disrupting trophic positions and destabilizing food webs in midinvasion lakes. Second, food web stability increases when apex predators are supported by a balance of littoral- and pelagic-derived carbon (26). We found that native bull trout and other fishes increasingly relied on littoral foods as invasion progressed, which may have destabilized food webs and promoted their transition to lake trout dominance. Indeed, food web instability is a precursor to ecological state change (27), and biological invasions are known to yield alternative ecological states (24). Given that trophic dispersion dissipated in late-invasion lakes, it is likely that these food web changes ultimately produced a new ecological regime dominated by the invasive top predator and the functional loss of the native top predator.

We found that an invasive pelagic predator, lake trout, forced other fishes to increasingly rely on littoral resources in deep glacial lakes. This directional shift is converse to a previous study that showed invasive littoral predators caused native lake trout to increasingly rely on pelagic foods in Canadian lakes (13). Although trophic displacement has been documented for a variety of taxa (14), these complementary results demonstrate that the direction of trophic displacement is a function of the feeding habitat an invader occupies and provide

clear evidence that invasive predators can influence dominant energy pathways of native predators. Together, these results provide a basis for understanding and predicting the directional effects of invasive species on recipient food webs.

Trophic dispersion and displacement varied among fish species, suggesting different types of competitive interactions among species. Trophic dispersion was acute for most prey fish, with the greatest dispersion occurring 25 to 50 y following lake trout colonization. For prey fish, these disruptions likely increased exploitative competition, which promotes the persistence of dietary generalists at the expense of specialists (28). At the top of the food chain, however, invasive lake trout displaced native bull trout to a mesopredator role 25 to 50 y after colonization. During the same time period, lake trout consumed bull trout (about 14% of their diet) and their abundance increased relative to bull trout across invaded lakes, ultimately resulting in the functional extirpation of bull trout in late-invasion food webs. Together, these findings suggest that interference competition and predation are the primary mechanisms that prevent these species from coexisting after lake trout invasion (29).

Ultimately, protecting entire landscapes from biological invasions may be needed to sustain native biodiversity and ecosystems. This strategy may require eliminating the introduction of invasive species, including nonnative fish-stocking programs, and using innovative biosurveillance monitoring techniques, such as environmental DNA (30), for early detection of potential invaders. For the restoration of invaded ecosystems, our findings emphasize the need to implement proactive control efforts, particularly during colonization and early stages of establishment, to avoid food web disruptions that may be difficult to reverse. This study provides a better basis for predicting ecosystem impacts of species invasions and can be used for strategic planning of conservation and mitigation efforts across entire ecosystems.

## Materials and Methods

**Study Systems.** The study area consisted of nine natural lakes and one reservoir (collectively called “lakes” throughout this article) west of the Continental Divide in northwestern Montana, USA (*SI Appendix*, Table S2). These oligotrophic, dimictic lakes are in forested and undeveloped watersheds on US public lands, like state and national forests and parks. Study lakes were classified into three categories based on their history of lake trout invasion: 1) reference, 2) midinvasion (i.e., middle), and 3) late invasion (*SI Appendix*, Table S2). Reference lakes have a native fish assemblage and have no lake trout (current conversion, 0). Midinvasion lakes have sympatric bull trout and lake trout populations and current (i.e., 2019 or most recent available) conversion between 0.4 and 0.8. Late-invasion lakes also have sympatric bull trout and lake trout populations but have current conversion values greater than 0.8. “Conversion” is analogous to lake trout dominance.

**Food Web Sampling.** All samples were collected between June and October in 2017, 2018, and 2019. Fish were collected with sinking and floating mono- and multifilament gill nets, littoral fyke nets, benthic hoop nets, hook and line, and backpack electrofishing concurrent with US National Park Service and Montana Fish, Wildlife & Parks fisheries surveys. Gill nets were 38-m-long by 2-m-deep panels of 10- to 100-mm bar mesh. Fyke nets had 8-m leads and 4-m hoop sections with one 75-mm vertical trapping pane, one 90-mm throat, and black 6-mm stretch mesh. Benthic hoop nets were 4 m long with two 90-mm throats and black 6-mm stretch mesh. Fyke and hoop nets were deployed in 12-h increments. Electrofishing was conducted in shallow water along lake shores using a Smith-Root LR-24. Animal (fish) sampling was conducted by US National Park Service and Montana Fish, Wildlife & Parks management agencies during routine monitoring surveys in accordance with agency animal use and care protocols. Bull trout collections were authorized with a special collection permit (Section 10) issued by the US Fish and Wildlife Service.

**Data Availability.** Datasets generated during and/or analyzed during the current study, an annotated R script for this study’s analyses, and an R markdown are available in Dryad at <https://doi.org/10.5061/dryad.z34tmpgdt>. The stable

isotope data reported in this study have been deposited in Dryad (<https://doi.org/10.5061/dryad.z34tmpgdt>) (31).

**ACKNOWLEDGMENTS.** This study was supported by the US Geological Survey (USGS) Biological Threats Program and The University of Montana's Flathead Lake Biological Station (FLBS). This research was conducted in collaboration with the US National Park Service, USGS, Montana Fish, Wildlife & Parks, US Forest Service, US Fish and Wildlife Service, and FLBS. We thank C. Kolar Tam (USGS) and T. Bansak (FLBS) for funding

support. We thank V. D'Angelo, J. McCubbins, C. Downs, L. Rosenthal, E. Schick, J. Matthews, D. Six, C. Fredenberg, J. Vanderwall, B. Weber, Z. Ren, and A. Baumann for field, laboratory, and logistical support. We thank C. Downs and J. McCubbins of the US National Park Service for providing monitoring data from Glacier National Park. We thank J. Giersch for assistance with the figures. A portion of the work contained herein comes from the thesis of C.A.W. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.

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