Aquatic Conservation: Marine and Freshwater Ecosystems

WILEY

ARTICLE OPEN ACCESS

Food Web Properties and the Type of Invasive Species Make the Ecosystem Vulnerable to Invasion

Tiina Sävilammi[1,2] | Silva Uusi-Heikkilä[1,2] | Anna Kuparinen[1]

[1]Department of Biological and Environmental Sciences, University of Jyväskylä, Jyväskylä, Finland | [2]Department of Biology, University of Turku, Turku, Finland

Correspondence: Anna Kuparinen (anna.k.kuparinen@jyu.fi)

Received: 11 June 2025 | **Revised:** 16 March 2026 | **Accepted:** 17 April 2026

Keywords: alien species | allometric trophic network model | anthropogenic change | aquatic ecosystem | network topology | niche model | simulation

ABSTRACT

Invasive species have long been acknowledged as potentially severe dangers to native ecosystems. Although some work has also been done with empirical food webs, more information is still needed to shed light on the cascading effects of invasive species in aquatic ecosystems. In this study, we used an extended niche approach to generate artificial food webs with multiple trophic species and variable parameters. We extended the niche approach by adding several age groups for the top trophic species (fish) to generate food web structures resembling those found in natural environments. Finally, we added an invader species with randomized parameters to each web. We used allometric trophic network (ATN) modelling to simulate 200 years of species biomass changes with and without the invader in the ecosystem. Fish biomasses and old age groups changed the most, with a response that was often a decline in the biomass. The change was predicted by food web depth (the number of feeding levels from the primary producers to the top predators in the ecosystem) and by the magnitude of ecosystem-level changes caused by invasion. Both the properties of native species and the invader, such as the trophic level and direct centrality (specialist/generalist feeding) and indirect centrality (cascading effects), affected the outcome. High Jaccard's similarity between the invader and the native species also predicted a negative impact on the top fish predators.

1 | Introduction

Invasive species can have significant negative effects on aquatic ecosystems, causing ecological damage through biodiversity loss and disruption of ecological interactions. For example, the presence of invasive species can reduce the richness of native species and modify ecosystem processes by altering trophic interactions and food web dynamics (Hui and Richardson 2019; Pyšek et al. 2020). The cascading effects caused by invasive species may lead to ecological imbalances by top-down (predation) or bottom-up (production) regulation of lower or higher trophic levels, respectively (David et al. 2017). Besides altered ecosystem structure and functioning, these changes in population dynamics can result in substantial economic damage. Some national-scale studies, as reviewed by Marbuah et al. (2014), have resulted in estimates of the impact of invasive species on the economy that range from 0.01% to 12% of gross domestic product and between 0.4 and 117 billion USD per country. Thus, effective monitoring and management strategies are crucial to mitigate adverse ecological and economic effects, but doing so requires solid, quantitative predictions about the impacts of invasions.

Previous studies have highlighted the crucial role of the food web structure in determining how cascading effects alter the outcome of a food web invasion (Hui and Richardson 2019). Doizy et al. (2018) used a generalized food web model to quantify the impacts of four virtual invasive species on a small British offshore island and found that some native species were at risk owing to a range of invasive species that was wider than had been previously believed. However, the network approaches to modelling complex food webs depend on the quality of model parametrization. Simulations based on food webs that have been generated by algorithms can be utilized to obtain theoretical insights into the effects of invasion across a wide range of generic food webs with unique topologies. Such generic food webs may provide mechanistic explanations of the processes that shape the species dynamics as well as provide valuable insights for conservation and management strategies.

The classic niche model, originally formulated by Williams and Martinez (2000), may be a valuable method for creating generic food webs that resemble empirically solved food webs. Furthermore, food web generation with the niche model does not require extensive parametrization because it incorporates only two parameters that are used in the construction of food webs: The number of trophic species (S) and the target connectance (C), which describe the fraction of all possible links that are realized in a food web. In the original niche model, each node of the graph represents a trophic species, which may consist of one species or multiple species that have similar functional roles. Fish species, however, often have age groups with distinct body sizes and, thereby, differences in their ecological roles and trophic interactions. The niche model has recently been extended by the incorporation of age classes interconnected by biomass flow through ageing and reproduction (Bland et al. 2019; Nonaka and Kuparinen 2021). Implementing age structure can be particularly important for capturing sufficient realism in the feeding interactions and reproductive capacity of fish species when studying commercially or conservationally important invasive or native fish species (David et al. 2017).

Both the invader properties and the properties of the recipient system can provide useful predictions for invasion success and whether the invasion becomes low impact (co-existing with the native species) or high impact (displacing the native species). For example, an invasive carp has been demonstrated to cause major bioturbations and to alter bottom-up processes in the River Po, Italy (Patonai et al. 2026), whereas the introduction of an apex predator can collapse native fishes, as was demonstrated in Lake Gatun, Panama (Sharpe et al. 2017). What comes to network topological features, such as food web depth and complexity, and the level of natural oscillations may also predict altered food web robustness and disturbances such as invasions (Thébault and Fontaine 2010; Romanuk et al. 2017). As another example, high web connectance may decrease the initial invasion probability but increase the consequences of successful invasions (Romanuk et al. 2017).

Different centrality indices can be used to identify potentially highly influential trophic species (Dunne et al. 2002) and successful invaders (Romanuk et al. 2009) in food webs. The direct centrality of the invader is a property that defines whether it is a specialist (feeding only on a few species) or a generalist (feeding on many species). The effectiveness of generalist invaders over those with a specialist role has been repeatedly recognized as a key property predicting invasion success, along with other network topological properties, such as the relatively low trophic level of the invader in the recipient web (Romanuk et al. 2009, 2017; Lurgi et al. 2014). In contrast, indirect centrality measures may be more efficient in defining keystone species, which have the ability to alter the abundances of many other species and have cascading effects on the invaded ecosystem (Jordán et al. 2007).

Invader impact may also interact with other properties of the recipient systems. For example, the effect of the trophic position of the invader on the food web connectivity may contribute to the predicted invasion success (Romanuk et al. 2017). As another example, an invader with low taxonomical distinctivity (i.e., an invader with closely related taxa in the invaded ecosystem) inhabiting an aquatic system may have a smaller effect than a taxonomically novel invader would (Ricciardi and Atkinson 2004). This may be explained by the prior co-evolution of the native species in the ecosystem, whereby they have already adapted to functionally similar species in the ecosystem. Taxonomical distinctivity has been suspected to have similar effects as ecological distinctivity, which means the functional similarity between the invader and the native species (Ricciardi and Atkinson 2004).

Some native species may be more vulnerable to an invasion than others are. For example, a recent study that utilized allometric trophic network (ATN) modelling predicted that a hypothetical invasion by a generalist fish, Amur sleeper (*Perccottus glenii*), would affect the top predator fish more heavily than it would the lower trophic level species in the empirically parametrized Lake Võrtsjärv food web (Kuparinen et al. 2023). As the higher trophic level fish species both stabilize entire ecosystems through top-down control and are economically important as well as a notable source of food for human consumption, invasion patterns such as the one predicted in Lake Võrtsjärv can have severe consequences, particularly for native fishes that are exposed to fishing at the same time that they are affected by invasion and potential other stressors.

The aim of the present study is to generalize the theory surrounding the observations made in the Lake Võrtsjärv food web model (Kuparinen et al. 2023). We upscale this single, albeit empirically based observation across a range of food webs and invader types, thereby developing the theory of food web dynamics in the context of aquatic invasions applicable particularly to temperate lakes such as Lake Võrtsjärv. To this end, we investigate the effects of an invader on the aquatic food web structure, dynamics and biomass distribution. We hypothesize that (i) the impacts of invasion adversely affect the native fish community and (ii) alter the properties of the invaded food webs. We study this by exploring the responses of the food webs generated with an age-structured niche model extension (Bland et al. 2019) using a range of alternative food web topologies and invader properties. We define the invasion success through the invader biomass, specifically whether it declines after being introduced to the stabilized lake food web (unsuccessful invasion) or whether it stabilizes at the introduced density or starts to increase (successful invasion).

2 | Methods

2.1 | Food Web Generation

To generate food webs, we extended the original niche model (Williams and Martinez 2000) using an in-house Matlab v. R2020b implementation (Bland et al. 2019). The food webs were created according to the original niche model by generating $S = 50$ trophic species (hereafter species) with a targeted web connectance of $C = 0.15$ (these values were chosen to be in the same order of magnitude as in Lake Võrtsjärv but not too specific for this model system). Each trophic species was then assigned a random niche value (n) between 0 and 1 from a uniform distribution. Then, each species was randomly assigned the width of a range (r) from a beta distribution with parameters alpha = 1 and beta = $(1 - 2C)/(2C)$, where C is the connectance of the food web and the mean value of the distribution is $2C$, to obtain a food web with a connectance value close to the targeted C. The range width r modifies the specialist/generalist aspect of each species. Finally, each species was assigned a centre of range (c), which depends on the species' niche value and is sampled from a uniform distribution between $r/2$ and n. The species are assigned as prey if their niche value is in the predator's centred range. The species that do not have any prey were considered producers, and the species with higher trophic levels were considered consumers. We set the species with the lowest niche value to $n = 0$ in the webs, where no basal species was automatically generated by the web generator (Williams and Martinez 2000). We repeated the food web generation by discarding webs until basic requirements were met. We discarded the generated food webs that had a connectance error of more than ±2.5%, or if the minimum number of possible links exceeded the maximum number of possible links. We also discarded food webs with disconnected groups of species, food webs with species that were not connected to the basal species and webs with cyclic eating patterns (i.e., Species B is eating Species A that is eating Species B).

Then, we extended the food webs by adding fish with multiple age groups. We used the niche model extension by Bland et al. (2019) to generate three species of fish with four age groups each. The new age groups of fish were assigned niche values, ranges and the centres of ranges by generating new niche-type food webs with the number of species identical to the age-structured food webs and by replacing the fish of the original food webs with the new age-grouped species. Age groups of fish without any prey (excluding possible cannibalism) were assigned to the closest possible species as prey based on the niche value and the centre of range values. For further information on food web generation, see Williams and Martinez (2000) and Bland et al. (2019).

After the food web construction, we assigned several parameters for each species. First, we calculated the short-weighted trophic level (average over the shortest path trophic level and the prey-averaged trophic level) of each species (Williams and Martinez 2004; Carscallen et al. 2012). We calculated the predator–prey body size ratio (Z) for consumers following the log-normal distribution (Table 1). We then generated per-species body masses (M_c) based on trophic level and predator–prey size ratios (Table 1). We set the assimilation efficiency of the consumed resources to 0.45 and 0.85 for herbivores and carnivores, respectively (Brose et al. 2006). The fractions of 0.4 and 0.1 of the assimilated carbon of consumers contributed to growth (f_a) and the maintenance of basic bodily functions (f_m), respectively (Boit et al. 2012; Kath et al. 2018). We set the growth season of each year to 100 days and the total carrying capacity to 540,000 weight units. We set the parameter q of the functional response to 0.2 to give the Holling Type III response of a predator's consumption rate at different prey densities (Nonaka and Kuparinen 2021). Feeding parameters were assigned according to Bland et al. (2019).

Each generated food web was then simulated through time by running the ATN model (Brose et al. 2006; Kuparinen et al. 2016; Bland et al. 2019). ATN models help explain between-species interactions by building on trophic predator–prey interactions and population dynamics depending on species' body size and metabolic type (here: producer, consumer or fish). First, we simulated the biomass changes of the food webs for a burn-in period of 1000 years to allow the species biomasses to reach equilibrium. We then added an invasive species to each food web. We set the initial body mass of the invader as the average body mass of the species in the food web. We used uniform distributions between 0.3 and 0.9 to sample the invaders' niche values from, uniform distributions between 0.05 and 0.4 to sample the invaders' ranges from and uniform distributions between 0.1 and the invader niche values to sample the centres of ranges of the invaders (Figure S1). Based on those variables, we used the niche model rules to assign prey and predator species of the invader within each food web (Williams and Martinez 2000). The feeding parameters of the invader followed those of Bland et al. (2019) by assuming that the invader was a consumer. This assumption was plausible as the invader's body size reflected the average body size in the food web and, thus, was not among the top fish predators. To prevent unconnected invaders, a species with niche value closest to the range of the invader was set as prey for the invader in the rare cases where no prey items were otherwise assigned to the invader. After the invasive species was added, we simulated the ecosystem for a test period of 200 years. To compare the invaded scenario to a scenario without the invasion, we also simulated a reference period of 200 years of equilibrium without the invader. We generated approximately 3000 food webs. The reference webs were identical to the invasion scenario in terms of the initial biomasses and species links, other than those including the invader.

2.2 | Food Web Responses to Invasions

To evaluate whether the total biomass of the ecosystems was altered in response to the invasion, we calculated the joint total biomass of all the species in the ecosystem and by species metabolic type (producer, consumer, fish) under the invaded and the reference simulation scenarios. We calculated the total ecosystem biomass at the start of the simulation and at the end by averaging over years 1–50 and 150–200, respectively (Table 1). We calculated (percentual) biomass change between invaded and non-invaded scenarios and used t-tests with Bonferroni correction to evaluate if the change was significant between the scenarios with and without the invader biomass (Table 1). We determined that the invasion was successful in a web if the invasive species' biomass persisted or increased during the invaded scenario simulation and included only the webs with successful invasions in the analysis.

TABLE 1 | A reference table of variables estimated from the simulated food webs, from comparisons between food webs from invaded and reference scenarios, and from individual trophic species in the food webs. For exact equations, see the associated reference.

Comparison type	Variable	Definition
Within-scenario variables	Start biomass	Average biomass over years 1–50
	End biomass	Average biomass over years 150–200
	(Percentual) biomass change	(End biomass – start biomass)/start biomass
	Total biomass change	(Sum of end biomasses – sum of start biomasses)/sum of start biomasses
	Biomass oscillation	CV (trophic species biomass over years)
	Biomass oscillation of a metabolic type	Median of the biomass oscillations of the trophic species with a specified metabolic type
	Modularity	The level of modularity in the food web
Between-scenarios variables	End biomass response	End biomass in the invaded scenario/end biomass in the reference scenario
Trophic species properties	Metabolic type	Metabolic rates were based on body size following Brose et al. (2006).
	Trophic level (*TL*)	Short-weighted trophic level; the average of the shortest trophic level and prey-averaged trophic level (Williams and Martinez 2004; Carscallen et al. 2012)
	Predator:prey body mass ratio (*Z*)	*Z* was generated for consumers from log-normal distributions using log-transformed mean body weights of 5000 and 100 weight units for fish and invertebrate consumers, and standard deviations of 10 for both metabolic types. Producers were set with $Z = 0$ (Brose et al. 2006).
	Consumer body mass (M_C)	Body masses of consumers were generated after defining *TL* and *Z* using function $M_c = Z^{TL}$. The resulting body masses were relative to the body masses of the basal species (Brose et al. 2006).
	In-degree	The number of incoming links (predators) (Vesterinen et al. 2021)
	Out-degree	The number of outgoing links (preys) (Vesterinen et al. 2021)
	In-closeness	The lengths of minimum paths from a given trophic species to all upstream (prey) species (Vesterinen et al. 2021)
	Out-closeness	The lengths of minimum paths from a given trophic species to all downstream (predator) species (Vesterinen et al. 2021)
	Betweenness	How frequently a trophic species is on the shortest path between two other species (Vesterinen et al. 2021)
	PageRank	A variant of EigenCentrality, invented by the founders of Google. It is based on incoming links (Vesterinen et al. 2021).
	EigenCentrality	Centrality measure, which ranks higher the nodes that are connected to high-ranking nodes. In- and outgoing links are equal (Vesterinen et al. 2021).
	Jaccard's similarity to invader	The level of similarity between the invader and native species, calculated by comparing the number of identical trophic interactions (feeding links) between each of the two species and the other species of the corresponding food web to the number of trophic interactions in either of the species by dividing identical trophic interactions by the number of trophic interactions observed in at least one of the species
	Minimum Jaccard's similarity of invader to native species	The average similarity of invader to the top 10% quantile of the most topologically similar native species

To evaluate the level of biomass oscillation of each species in the webs, we calculated the per-trophic species coefficient of variation (CV) for the yearly biomasses. We also calculated the median oscillation over each metabolic type (consumer, invertebrate producer of fish) for each web.

We assessed the effects of various species-specific explanatory variables to the biomass response to invasion. We first rank-scaled all numerical variables. We included the random effect of food web identity and multiple fixed explanatory variables describing the trophic positioning of each species in the webs using a linear mixed effects model (implemented in package lmerTest v. 3.1.3). We included information about whether each species was a direct prey or predator of the invasive species; in- and out-degree; in- and out-centrality; betweenness; EigenCentrality; PageRank; trophic level (relative to maximum trophic level in the web); and Jaccard's similarity to the invader (Table 1). After establishing the initial model estimates, we excluded variables causing collinearity (variance inflation factor (VIF) > 5; implemented in car v. 3.1.2 package) and non-significant explanators. We estimated non-parametric 95% confidence intervals for the estimates by resampling the subsets using 100 bootstrapping replicates with replacement.

We used several food web– and invader-specific properties to identify characteristic features of the food web topology and the invader species that were associated with the biomass response in the age groups of fish. To this end, we divided the food webs based on each food web– and invader-specific property into categories of 'low', 'average' and 'high' impacts. We repeated the final linear mixed-effect model inference for each 'low' and 'high' category assigned by each food web- and invader-specific property. We added metabolic type as an explanatory variable to estimate the age group responses of fish in the subsets of food webs in the 'low' and 'high' categories of the studied explanatory variables. We estimated non-parametric 95% confidence intervals by 100 bootstrapping replicates of the food webs with replacement.

3 | Results

3.1 | Food Web Generation

Excluding the invader, the median number of producer and non-vertebrate consumers generated was 10 (95% CI [10, 11]) and 36 (95% CI [36, 37]), whereas the number of fish species generated was always three, and the number of age groups for the fish was always four. Species abundance inversely correlated with total biomass, which had a median of 69.8% (95% CI [69.5%, 70.1%]), 29.3% (95% CI [29.0%, 29.7%]) and 0.4% (95% CI [0.3%, 0.4%]) in producers, non-vertebrate consumers and fish, respectively. The median invasive species biomass at the end of the simulation was 0.7% (95% CI [0.66%, 0.72%]) of the food web biomass. The invader persisted in 88.7% of the food webs.

3.2 | Food Web Responses to Invasions

The total biomass of the native species decreased significantly in the invaded food webs in comparison with the reference scenario (on average, 0.8%; $t_{2680} = -2.2$, Bonferroni-corrected $p = 0.05$), but the difference was non-significant after including the biomass of the invader ($p = 0.79$). However, variability over the 200-year simulation increased in response to the invasion: The standard deviation of the biomasses of the native species increased from $< 0.01\%$ to 0.2% in the invaded scenario (Figure 1A). The prey species biomasses of the invasive species decreased in the successfully invaded food webs. Where the invasion failed (i.e., the invader biomass decreased from the initial 1000 units), only a small average decline in the combined biomasses of the invaders' prey species was observed in the food webs. In contrast, where the invasion was successful, a significant decline in prey biomass was found in the food webs. The average combined biomass of the invasive species' predators remained unchanged in the food webs where the invasion was successful, whereas a slight decrease was observed in webs where the invasion failed (Figure S2).

The average biomass change per species over time was altered (either increased or decreased), especially among fish in the invaded food webs (Figure 1B). Similarly, an increase in biomass oscillations (mean CV of the species biomasses over time) was

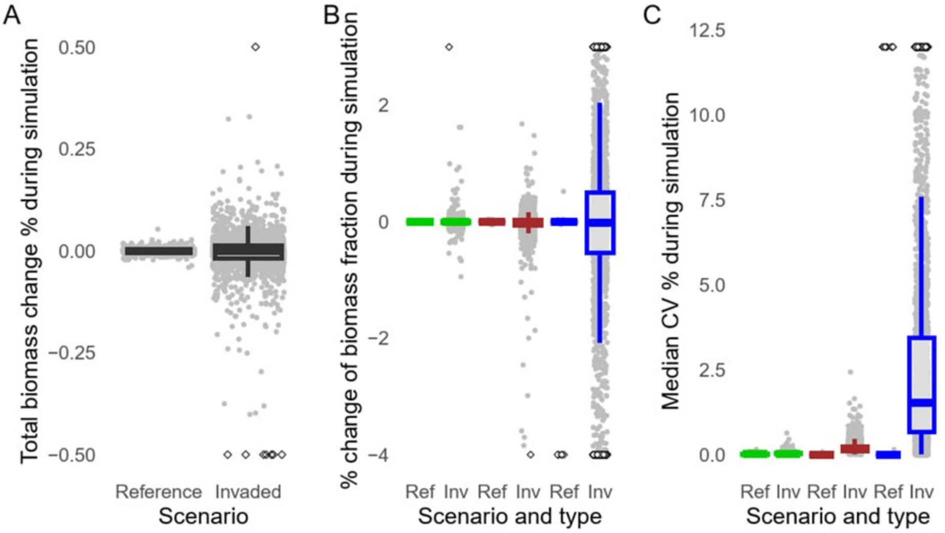

FIGURE 1 | Biomass changes of the native species between simulated food webs. Estimates from the reference scenario simulations ('Ref') reflect the natural oscillations, whereas estimates from the simulations under invaded ('Inv') scenario add the oscillations caused by the invasion. Total percentual biomass change in the food webs during simulations (A). Changes (B) and median CVs (C) of the biomasses in the food webs by the metabolic type (producers in green, consumers in brown and fish in blue) during simulations. Note that the *y*-axis scales are capped at maximum values of the axes and outlier observations indicated with diamond-shaped points.

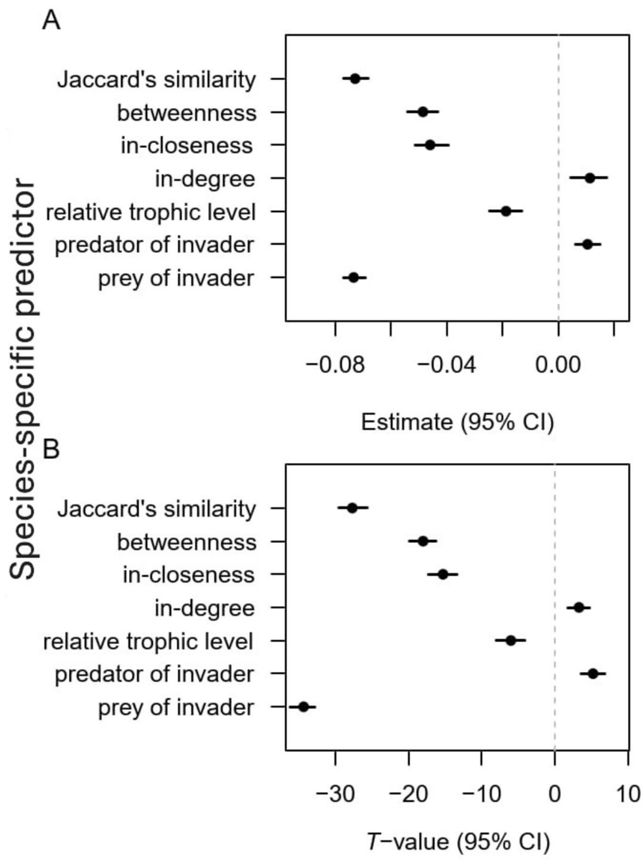

FIGURE 2 | Characteristics of species that explain their biomass responses to invasions. Estimated effect sizes (A) and the associated *t*-values (B) of multiple fixed factor predictors ($p < 0.05$ for each; *y*-axis) of the rank-scaled end biomass responses to the invasion, obtained from the linear mixed-effect model.

observed in response to the invasions and the magnitude differed among the metabolic types. The change was close to zero in the reference food webs, whereas increases were observed in producers (from 0.02 to 0.44), in consumers (from 0.01 to 1.44) and in fish (from 0.22 to 9.79; Figure 1C).

We excluded PageRank and eigenvalue based on VIF, and out-degree and out-closeness based on non-significant effects as explanatory variables in the linear mixed-effect model. The final model was *biomass response* ~ (1|*web identity*) + *is prey of invader* + *is predator of invader* + *relative TL* + *in-degree* + *in-closeness* + *betweenness* + *Jaccard's similarity to invader*. The estimated effects and *t*-values of trophic species-specific predictors are presented in Figure 2.

The model estimates for the fish age groups are presented with the bootstrapped 95% confidence intervals in Figure 3. Estimates are presented separately for the food webs categorized as 'low' and 'high' based on the levels of the studied food web- and invader-specific variables.

4 | Discussion

In the present study, invasive species had a variable range of prey species (specialist/generalist predator) and trophic levels. The use of variable parameters for both the invasive species and the recipient food web was motivated by our aim to capture the inherent variability and unpredictability in complex biological systems. This approach enhanced the ecological generality of our simulations, allowing for a broad examination of alternative outcomes, and it ensures that our findings are robust and applicable across diverse invasion scenarios and food web configurations. Indeed, in the simulated food webs, the responses of successful invasions were unpredictable. Invasion transiently increased variation in the whole system, affecting the total biomass of the web. Invasive species biomass replaced some of the biomass of the native species. The oscillations after the invasion were most evident in the old fish, which are often positioned at the highest trophic levels. We therefore hypothesized that invasive species can severely affect the fish age groups most relevant for reproduction and for commercial use. Indeed, this has been observed in the simulated Lake Võrtsjärv food web, where invasion by Amur sleeper had the strongest effect on the top predatory fish (Kuparinen et al. 2023). Eventually, a successful invasion may also have evolutionary consequences, but due to the complexity of the ecological system alone, we restricted the dynamics to ecological ones. Similarly, (i) we did not consider external environmental variations but limited our analyses to inherent variability in the dynamic complex systems in order to detect species and food web properties potentially responsive to invasion success (Figure 3) without masking these patterns with external variations; (ii) our analyses apply across the simulated parameter space detailed in Section 2. This is because our primary aim was to upscale and generalize the findings by Kuparinen et al. (2023) in the temperate Lake Võrtsjärv and, within this framework, to understand the mechanisms underlying the invasion success. Therefore, we acknowledge that these choices pose limitations to the study, and a more universal theory (if such can be found) warrants future research. From a theoretical ecological perspective, however, our results can be considered conservative, as our invasive consumer species was not as efficient of a feeder as an invasive fish would have been (such as Amur sleeper in Kuparinen et al. 2023).

Among the species properties that contributed to the direction and magnitude of biomass change in response to invasion, regardless of the ecosystem, those that were particularly severely affected were species with high Jaccard's similarity to the invader. This was in concordance with prior studies on the invasion outcomes with empirical data, reviewed by David et al. (2017). Not surprisingly, the average biomass of the invader prey species decreased by over 7%, and that of the predator species of the invader increased by nearly 2%. After considering the direct interactions caused by the invader, only the positive direct in-degree effect, but not the out-degree (specialist/generalist) effect of the native species, persisted. This means that the abundances of the species with multiple predators increased slightly in response to the invasion. It is a long-acknowledged concept that specialist species may be vulnerable to ecosystem perturbations and, as the world continues to face anthropogenic environmental changes, generalists are replacing those specialists (Clavel et al. 2011). In our food web simulation approach, the increased explanatory power of indirect centrality indices in comparison with direct out-degree

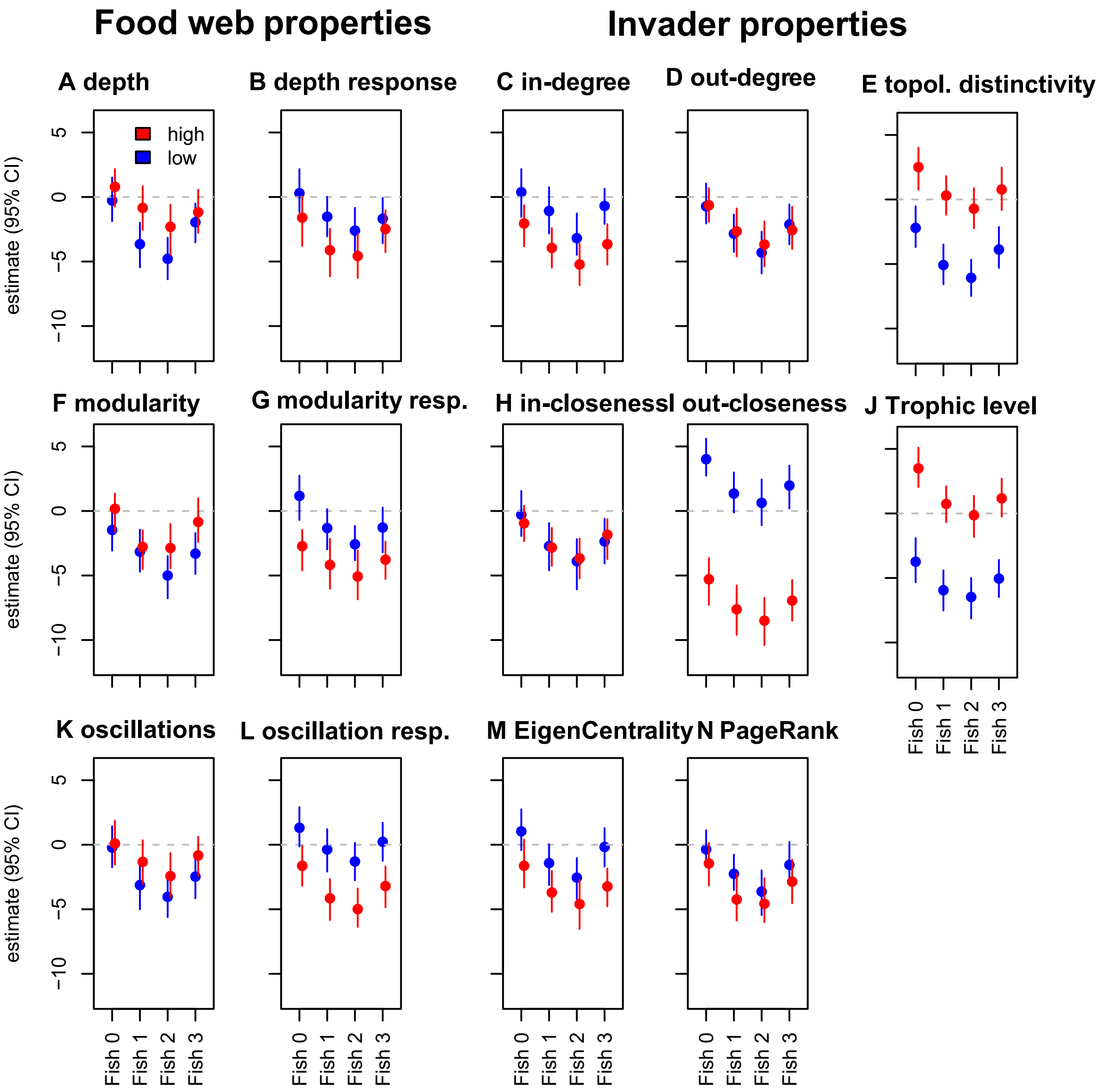

FIGURE 3 | Estimated rank-scaled effect sizes of the fish age groups with the response presented as percentual biomass response to the invasion (ranging from 10% decrease to 5% increase in fish age group biomass). The effects are estimated separately for subsets of food webs belonging to 'low' (blue) and 'high' (red) categories based on several properties describing the food web topologies and the invasive species. Properties describing food web topology are the reference food web depth (mean trophic level in a web; A) and the change in the food web depth caused by invasion (B); food web modularity (F) and the change in the modularity caused by the invasion (G); the level of natural biomass oscillations (K) and the change in the biomass oscillations caused by the invasion (L). Properties describing the invasive species are the invader in-degree (C) and out-degree (D); minimum topological distinctivity between the invader and the native species (E); the in-closeness (H) and out-closeness (I); the relative trophic level (J); the EigenCentrality (M); and the PageRank (N).

(the level of specialism/generalism of a species) was a more powerful explanator for the dynamics of the species under perturbations. Indirect centrality tended to be associated with the biomass decrease of the topologically central species. This observation complements prior studies, which have identified generalist invaders at relatively low trophic levels as a particularly severe threat to general ecosystem stability (Romanuk et al. 2009, 2017).

When considering the food web properties, we found only suggestive associations between food web topology prior to the invasion and the invasion response in fish biomasses, as the fish in the shallow webs were somewhat more affected than the fish in deep food webs. Prior studies on food web modularity and robustness have led to contradictory results and may also depend on other parameters (Thébault and Fontaine 2010; Garay-Narváez et al. 2014). However, we found that the biomass of fish tended to decrease in the ecosystems where invasion increased web depth, complexity (modularity) or the level of oscillations. Thus, we confirmed the prior research, which has suggested that invasions may have the capacity to profoundly shape the food web structure (Romanuk et al. 2009, 2017; Lurgi et al. 2014; David et al. 2017).

As stressed by Thomsen et al. (2014), the consequences of invasion should be evaluated separately for ecologically different native species. Confirming our hypothesis, several invader properties predicted well the survival of fish populations in the system. Invaders that were topologically most distinct from the native species had clearly more detrimental effects on the fish populations than did invaders that were similar to native species (Jaccard's similarity). This phenomenon is well supported by prior research, starting from niche theory, which suggests that if two species occupy the same niche (i.e., they utilize the same resources in the same habitat), one species will exclude the other (Webb et al. 2002). Although we acknowledge that the situation is more complex in nature due to phenomena such as niche shifts and differing assimilation efficiencies of prey items (Pianka 1973; Weber 1999; Pacioglu et al. 2019), this result demonstrates that the model can produce patterns similar to those seen in nature and it has been suggested that pre-trained ecosystems may tolerate the new species relatively well (David et al. 2017). The need for a more thorough survey of the niche overlap has also been acknowledged by, for example, Pacioglu et al. (2019) (accounting assimilation efficiency). We suggest that the niche overlap of co-existing species should be explored more carefully than by simply accounting for the direct prey species.

High direct and indirect centrality and the relatively low trophic level of the invader have been suggested to predict successful invasion (Romanuk et al. 2009, 2017; Lurgi et al. 2014). These were also the properties that were the most detrimental to the fish populations in the present study, decreasing fish biomasses by as much as 10%. Although in-centrality and trophic level were not problematically correlated in the VIF analysis, invaders with high direct in-centrality are often species at relatively low trophic levels, which serve as prey for many other species and thus have indirect effects on fish populations. Notably, only direct in-centrality (in-degree) and indirect out-centrality (out-closeness) of the invader had a negative effect on fish populations. The detrimental effect of the invaders with high direct in-centrality (many predators) is cryptic and suggests that invasion may have unpredictable outcomes in the ecosystem. High indirect out-centrality means that the invader has many interacting species at lower trophic levels, which may be either direct prey items or indirect ‘preys of preys’, resulting in widely cascading effects on multiple downstream prey levels. Although generalist invaders have been stated as particularly harmful to the ecosystem, our observation suggests that also cascading effects on the downstream species (out-closeness) should be taken into account when assessing the potential impacts. Overall, our study complies with the observations that the invasion by certain species may alter the whole ecosystem through cascading effects. For example, invasive crabs and whelks increase the mortality of native oysters and disrupt the diversity of the ecosystem by triggering trophic cascades (Kimbro et al. 2009). It has been observed that the invasion by zebra mussel (*Dreissena polymorpha*) caused increased phytoplankton biomasses and, therefore, changes in the top predator ecology (Hirsch et al. 2013). Interestingly, invasion by a low out-closeness invader (extreme specialist) seemed to even increase fish abundances. A puzzling phenomenon was also that invaders with low trophic levels had a more negative impact on fish populations than did those at higher trophic levels. The diversity of native fish species has been previously reported to have altered the invasion success of the Common carp (*Cyprinus carpio*) in the experimental metacosm setup by Carey and Wahl (2010). Increased between-species competition among species at higher trophic levels may be the underlying explanation for this phenomenon.

5 | Conclusions

Biomasses of species at high trophic levels and the key players of the ecosystem were negatively affected by invasions. Although invasive species at the relatively high trophic positions often receive more attention, invasion by low trophic level species seemed to have more drastic effects on fish populations via indirect and cascading effects on lower trophic levels in the food web. We showed that food webs with more trophic levels and species that were topologically distinct from the invasive species were more robust against invasive species than were shallow webs and native species resembling the invader. Such observations provide particularly timely information now that the warming climate has been predicted to increase invasion success in food webs and ecosystems (Sentis et al. 2021). A future challenge for simulations exploring invasion success is therefore to explicitly incorporate abiotic drivers such as temperature (e.g., Eloranta et al. 2023) and to assess the role of such drivers in biological invasions. Nonetheless, our complex albeit theoretical framework provides a solid starting point for analyses and model extensions to incorporate additional factors such as abiotic forcing, eco-evolutionary feedbacks and also potential non-trophic interactions. Algorithm-based generic food webs (e.g., Williams and Martinez 2000; Bland et al. 2019) are instrumental to this end, because they capture the inherent variability and uncertainty associated with food web structures while also addressing the issue that solving empirical food webs is time consuming and sometimes not even feasible. Nonetheless, even if such empirically solved food webs are available, algorithm-based generic food webs are an ideal way to (i) test the consistency of empirically observed results with the simulated ones (e.g., Williams and Martinez 2000) and (ii) produce uncertainty estimates for the observed feedbacks.

Author Contributions

Tiina Sävilammi: methodology, visualization, formal analysis, writing – original draft, investigation. **Silva Uusi-Heikkilä:** writing – review and editing, conceptualization, investigation, supervision. **Anna Kuparinen:** writing – review and editing, writing – original draft, conceptualization, funding acquisition, investigation, supervision, project administration, resources.

Acknowledgements

AI was not used in the preparation of the manuscript. Open access publishing facilitated by Jyvaskylan yliopisto, as part of the Wiley - FinELib agreement.

Funding

This study was funded by the Research Council of Finland (project grant 317495 to A.K. and 325107 to S.U.-H.) and from the European Union‘s Horizon 2020 research and innovation programme under grant agreement No. 951963 (TREICLAKE). This project also received funding from the European Research Council (ERC) under the European

Union's Horizon 2020 research and innovation programme under grant agreement No. 770884 (COMPLEX-FISH).

Ethics Statement

The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The generated food webs and the codes used in data analysis are found in the Dryad repository: DOI: 10.5061/dryad.t76hdr885.

References

Bland, S., F. S. Valdovinos, J. A. Hutchings, and A. Kuparinen. 2019. "The Role of Fish Life Histories in Allometrically Scaled Food-Web Dynamics." *Ecology and Evolution* 9, no. 6: 3651–3660. https://doi.org/10.1002/ece3.4996.

Boit, A., N. D. Martinez, R. J. Williams, and U. Gaedke. 2012. "Mechanistic Theory and Modelling of Complex Food-Web Dynamics in Lake Constance." *Ecology Letters* 15, no. 6: 594–602. https://doi.org/10.1111/j.1461-0248.2012.01777.x.

Brose, U., R. J. Williams, and N. D. Martinez. 2006. "Allometric Scaling Enhances Stability in Complex Food Webs." *Ecology Letters* 9, no. 11: 1228–1236. https://doi.org/10.1111/j.1461-0248.2006.00978.x.

Carey, M. P., and D. H. Wahl. 2010. "Native Fish Diversity Alters the Effects of an Invasive Species on Food Webs." *Ecology* 91, no. 10: 2965–2974. https://doi.org/10.1890/09-1213.1.

Carscallen, W. M. A., K. Vandenberg, J. M. Lawson, N. D. Martinez, and T. N. Romanuk. 2012. "Estimating Trophic Position in Marine and Estuarine Food Webs." *Ecosphere* 3, no. 3: 1–20. https://doi.org/10.1890/ES11-00224.1.

Clavel, J., R. Julliard, and V. Devictor. 2011. "Worldwide Decline of Specialist Species: Toward a Global Functional Homogenization?" *Frontiers in Ecology and the Environment* 9, no. 4: 222–228. https://doi.org/10.1890/080216.

David, P., E. Thebault, 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. https://doi.org/10.1016/bs.aecr.2016.10.001.

Doizy, A., E. Barter, J. Memmott, K. Varnham, and T. Gross. 2018. "Impact of Cyber-Invasive Species on a Large Ecological Network." *Scientific Reports* 8, no. 1: 13245. https://doi.org/10.1038/s41598-018-31423-4.

Dunne, J. A., R. J. Williams, and N. D. Martinez. 2002. "Network Structure and Biodiversity Loss in Food Webs: Robustness Increases With Connectance." *Ecology Letters* 5, no. 4: 558–567. https://doi.org/10.1046/j.1461-0248.2002.00354.x.

Eloranta, A. P., T. Perälä, and A. Kuparinen. 2023. "Effects of Temporal Abiotic Drivers on the Dynamics of an Allometric Trophic Network Model." *Ecology and Evolution* 13, no. 3: e9928. https://doi.org/10.1002/ece3.9928.

Garay-Narváez, L., J. D. Flores, M. Arim, and R. Ramos-Jiliberto. 2014. "Food Web Modularity and Biodiversity Promote Species Persistence in Polluted Environments." *Oikos* 123, no. 5: 583–588. http://www.jstor.org/stable/24567499.

Hirsch, P. E., P. Eklöv, and R. Svanbäck. 2013. "Indirect Trophic Interactions With an Invasive Species Affect Phenotypic Divergence in a Top Consumer." *Oecologia* 172: 245–256. https://doi.org/10.1007/s00442-013-2611-1.

Hui, C., and D. M. Richardson. 2019. "How to Invade an Ecological Network." *Trends in Ecology & Evolution* 34, no. 2: 121–131. https://doi.org/10.1016/j.tree.2018.11.003.

Jordán, F., Z. Benedek, and J. Podani. 2007. "Quantifying Positional Importance in Food Webs: A Comparison of Centrality Indices." *Ecological Modelling* 205, no. 1–2: 270–275. https://doi.org/10.1016/j.ecolmodel.2007.02.032.

Kath, N. J., A. Boit, C. Guill, and U. Gaedke. 2018. "Accounting for Activity Respiration Results in Realistic Trophic Transfer Efficiencies in Allometric Trophic Network (ATN) Models." *Theoretical Ecology* 11: 453–463. https://doi.org/10.1007/s12080-018-0378-z.

Kimbro, D. L., E. D. Grosholz, A. J. Baukus, et al. 2009. "Invasive Species Cause Large-Scale Loss of Native California Oyster Habitat by Disrupting Trophic Cascades." *Oecologia* 160: 563–575. https://doi.org/10.1007/s00442-009-1322-0.

Kuparinen, A., A. Boit, F. S. Valdovinos, H. Lassaux, and N. D. Martinez. 2016. "Fishing-Induced Life-History Changes Degrade and Destabilize Harvested Ecosystems." *Scientific Reports* 6, no. 1: 22245. https://doi.org/10.1038/srep22245.

Kuparinen, A., S. Uusi-Heikkilä, T. Perälä, et al. 2023. "Generalist Invasion in a Complex Lake Food Web." *Conservation Science and Practice* 5, no. 6: e12931. https://doi.org/10.1111/csp2.12931.

Lurgi, M., N. Galiana, B. C. López, L. N. Joppa, and J. M. Montoya. 2014. "Network Complexity and Species Traits Mediate the Effects of Biological Invasions on Dynamic Food Webs." *Frontiers in Ecology and Evolution* 2: 36. https://doi.org/10.3389/fevo.2014.00036.

Marbuah, G., I.-M. Gren, and B. McKie. 2014. "Economics of Harmful Invasive Species: A Review." *Diversity* 6, no. 3: 500–523. https://doi.org/10.3390/d6030500.

Nonaka, E., and A. Kuparinen. 2021. "A Modified Niche Model for Generating Food Webs With Stage-Structured Consumers: The Stabilizing Effects of Life-History Stages on Complex Food Webs." *Ecology and Evolution* 11, no. 9: 4101–4125. https://doi.org/10.1002/ece3.7309.

Pacioglu, O., J. P. Zubrod, R. Schulz, J. I. Jones, and L. Pârvulescu. 2019. "Two Is Better Than One: Combining Gut Content and Stable Isotope Analyses to Infer Trophic Interactions Between Native and Invasive Species." *Hydrobiologia* 839, no. 1: 25–35. https://doi.org/10.1007/s10750-019-03990-8.

Patonai, K., A. Gavioli, M. Lanzoni, A. Hidas, and G. Castaldelli. 2026. "Fish Invasion Restructures Freshwater Food Webs, Facilitating New Invasions Over Three Decades." *Frontiers in Environmental Science* 13: 1727438. https://doi.org/10.3389/fenvs.2025.1727438.

Pianka, E. R. 1973. "The Structure of Lizard Communities." *Annual Review of Ecology and Systematics* 4, no. 1: 53–74. https://www.jstor.org/stable/2096804.

Pyšek, P., P. E. Hulme, D. Simberloff, et al. 2020. "Scientists' Warning on Invasive Alien Species." *Biological Reviews* 95, no. 6: 1511–1534. https://doi.org/10.1111/brv.12627.

Ricciardi, A., and S. K. Atkinson. 2004. "Distinctiveness Magnifies the Impact of Biological Invaders in Aquatic Ecosystems." *Ecology Letters* 7, no. 9: 781–784. https://doi.org/10.1111/j.1461-0248.2004.00642.x.

Romanuk, T. N., Y. Zhou, U. Brose, E. L. Berlow, R. J. Williams, and N. D. Martinez. 2009. "Predicting Invasion Success in Complex Ecological Networks." *Philosophical Transactions of the Royal Society, B: Biological Sciences* 364, no. 1524: 1743–1754. https://doi.org/10.1098/rstb.2008.0286.

Romanuk, T. N., Y. Zhou, F. S. Valdovinos, and N. D. Martinez. 2017. "Robustness Trade-Offs in Model Food Webs: Invasion Probability Decreases While Invasion Consequences Increase With Connectance." In *Advances in Ecological Research*, 263–291. Academic Press Inc.

Sentis, A., J. M. Montoya, and M. Lurgi. 2021. “Warming Indirectly Increases Invasion Success in Food Webs.” *Proceedings of the Royal Society B: Biological Sciences* 288, no. 1947: 20202622. https://doi.org/10.1098/rspb.2020.2622.

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, no. 2: 412–424. https://doi.org/10.1002/ecy.1648.

Thébault, E., and C. Fontaine. 2010. “Stability of Ecological Communities and the Architecture of Mutualistic and Trophic Networks.” *Science* 329, no. 5993: 853–856. https://doi.org/10.1126/science.1188321.

Thomsen, M. S., J. E. Byers, D. R. Schiel, et al. 2014. “Impacts of Marine Invaders on Biodiversity Depend on Trophic Position and Functional Similarity.” *Marine Ecology Progress Series* 495: 39–47. https://doi.org/10.3354/meps.

Vesterinen, M., T. Perälä, and A. Kuparinen. 2021. “The Effect of Fish Life-History Structures on the Topologies of Aquatic Food Webs.” *Food Webs* 29: e00213. https://doi.org/10.1016/j.fooweb.2021.e00213.

Webb, C. O., D. D. Ackerly, M. A. McPeek, and M. J. Donoghue. 2002. “Phylogenies and Community Ecology.” *Annual Review of Ecology and Systematics* 33, no. 1: 475–505.

Weber, M. 1999. “The Aim and Structure of Ecological Theory.” *Philosophy of Science* 66, no. 1: 71–93. https://doi.org/10.1146/annurev.ecolsys.33.010802.150448.

Williams, R. J., and N. D. Martinez. 2000. “Simple Rules Yield Complex Food Webs.” *Nature* 404, no. 6774: 180–183. https://doi.org/10.1038/35004572.

Williams, R. J., and N. D. Martinez. 2004. “Limits to Trophic Levels and Omnivory in Complex Food Webs: Theory and Data.” *American Naturalist* 163, no. 3: 458–468. https://doi.org/10.1086/381964.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** The distribution of (A) n, (B) r and (C) c parameters in the native and invasive species. **Figure S2:** The difference of the total biomass differences (difference of the summed biomasses of the prey and the predator species of the invader, measured from the end to the start of the simulation period) of the trophic species that were preys (‘prey’) or predators (‘pred’) of the invader in the food webs where invasive species density decreased (‘D’) and in the food webs where the invasive species density increased the most (‘I’). The proportion of food webs where the invasive species decreased over time was 15%, so the food webs where the invasive species increased over the 85% quantile were used as the matching size comparison group.