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Combining food web theory and population dynamics to assess the impact of invasive species

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The impacts of invasive species on resident communities are driven by a tangle of ecological interactions difficult to quantify empirically. Combining a niche model with a population dynamic model, both allometrically parametrized, may represent a consistent framework to investigate invasive species impacts on resident communities in a food web context when empirical data are scarce. We used this framework to assess the ecological consequences of an invasive apex predator (*Silurus glanis*) in peri-Alpine lake food webs. Both increases and decreases of resident species abundances were highlighted and differed when accounting for different *S. glanis* body sizes. Complementarily, the prominence of indirect effects, such as trophic cascades, suggested that common approaches may only capture a restricted fraction of invasion consequences through direct predation or competition. By leveraging widely available biodiversity data, our approach may provide relevant insights for a comprehensive assessment and management of invasive species impacts on aquatic ecosystems.

KEYWORDS

biological invasions, trophic interactions, trophic cascade, impact assessment, *Silurus glanis*

Introduction

Invasive species represent a major threat to biodiversity through the alterations or extinctions of native populations (Lockwood et al., 2013). Alternatively, invasive species can provide ecological benefits in specific cases possibly mitigating their negative impacts within recipient ecosystems (e.g., resources for native species; Schlaepfer et al., 2011). However, the empirical quantification of both negative (e.g., native population decreasing through predation; Mills et al., 2004) and positive impacts of invasive species (e.g., resource acquisition facilitation for native species; Albertson et al., 2021) toward resident species requires extensive field investigations involving important human and financial costs (Diagne et al., 2020). Moreover, identifying all possible interspecific interactions (direct and indirect) and quantifying their influences on native population abundances are particularly challenging to achieve through field investigations (Crystal-Ornelas and Lockwood, 2020). Consequently, modeling approaches can represent a keystone to circumvent these methodological constraints and forecast repercussions of biological invasions on resident populations (Kamenova et al., 2017).

Few quantitative methods allow predicting invasive species impacts on native populations, and mostly rely on the relationships between resource availability and their intake by consumers (Dick et al., 2014). This relationship has been updated by integrating consumer abundances (Dick et al., 2017), species propagule pressures (i.e., RIR = relative invasion risk; Dickey et al., 2018) or considering functional response ratios (i.e., FRR = attack rate/handling time; Cuthbert et al., 2019). Yet, these methods are not explicitly embedded in a dynamic perspective and have mostly addressed impacts of invaders on reduced communities in experimental conditions (Alexander et al., 2013; Barrios-O'Neill et al., 2014; Cuthbert et al., 2018), leaving a comprehensive assessment of invasive species impact *in-situ* on wide resident communities out of reach (Frost et al., 2019). However, noticeable invader impacts usually initiate from direct interspecific interactions (i.e., predation; Mills et al., 2004) but can also propagate along food webs, causing indirect repercussions called trophic cascades that can be especially frequent in aquatic ecosystems (Shurin et al., 2002; Carpenter et al., 2010). These ecological interactions are recognized to structure global biodiversity patterns across trophic levels (Zhang et al., 2018) and population dynamics and their disturbance may ultimately affect species assemblages and the whole ecosystem functioning (Terry et al., 2018; Frost et al., 2019).

Identifying direct and indirect ecological interactions between invasive species and resident communities would therefore be a prerequisite for quantifying invader impacts, yet their empirical assessment through traditional methods (e.g., stomach contents) remains challenging when considering the whole food web scale (i.e., primary producers to apex predator). To answer these methodological limitations, species body size is a widely used trait to infer trophic interactions, particularly in aquatic ecosystems (Petchey et al., 2008; Gravel et al., 2013; Pomeranz et al., 2019), as it allometrically relates to most species biological rates (e.g., respiration, reproduction; Brown et al., 2004) and population characteristics (e.g., trophic levels, abundances; Brucet et al., 2017). Trophic interactions could then be scaled up to population dynamic models to investigate species persistence toward destabilizing factors at the whole food web scale (Brose et al., 2006).

In this study, we used an approach combining an allometric niche model with a population dynamic model, both allometrically scaled, to grasp the diversity of impacts (direct/indirect, negative/positive) that invasive species can exert on wide resident communities (from primary producers to the apex predator) in aquatic ecosystems. More precisely, we reconstructed a non-invaded and an invaded food web by inferring trophic interactions among multiple species clusters (S = 58) in presence and in absence of an invader using an allometric niche model (hereafter called aNM; Vagnon et al., 2021). These interactions were then included in a population dynamic model, based on the model from Brose et al. (2006) that we modified by using alternative allometric parameterization, allowing to measure abundance changes of resident species over time in absence/presence of the invader with few empirical data inputs. We computed impact metrics supporting the classification of population abundance modifications and extinctions. Specifically, we distinguished positive or negative impacts on abundances (i.e., increases or decreases) and we characterized the ecological interactions involved in these modifications (i.e., predation, competition, trophic cascades).

We applied this approach to assess the ecological consequences of the recent invasion (~10 years) of the European catfish (*Silurus glanis*) in large peri-Alpine lakes that are representative of successful water quality restauration plans and biodiversity management which both could be threatened by new pressures originating from modifications of resident species abundances following invasive species introductions. In order to provide global analyses and results valuable for large peri-Alpine lakes, we applied our approach to a dataset including species co-occurring in Lake Bourget, Lake Geneva and Lake Annecy. By combining food web theory and a population dynamic model, we aimed to answer three major questions regarding the impacts that *S. glanis* could exert on a resident community typical of large French peri-Alpine lakes. First, we asked which *S. glanis* body size could cause the highest changes on species abundances. We hypothesized that large *S. glanis* (>100 cm) could induce the greatest magnitude in species abundance changes due to its highest position in the food web. We then focused at identifying whether direct or indirect negative ecological interactions (i.e., predation, competition and trophic cascade decreasing species abundances) could be balanced by indirect positive interactions (i.e., trophic cascades increasing species abundances). It was expected that the detrimental effects of *S. glanis* could be balanced by trophic cascades characterized by amplified species abundances at lower trophic levels. Overall, our study highlighted the possible complex consequences of a new invasive species in large peri-Alpine lakes.

Materials and methods

Species inventory

We used species inventories from the three largest peri-Alpine French lakes: Lake Annecy (45°51′ 41.489″ N, 6°10′ 2.364″ E), Lake Bourget (45°43′ 46.842″ N, 5°52′ 10.484″ E) and Lake Geneva (46°26′ 27.213″ N, 6°30′ 38.177″ E) originating from annual monitoring surveys (i.e., recording of environmental parameters and biodiversity samplings) and scientific reports (©SOERE OLA-IS, INRAE Thonon-les-Bains, SILA, CISALB, CIPEL; Rimet et al., 2020). As these lakes are highly similar in terms of biodiversity (Jacquet et al., 2014), species co-occurring in the three lakes (n = 118; from primary producers to large vertebrates) were retained to represent typical species of these ecosystems and were characterized by their taxonomy (i.e., subphylum, group, family, genus, species), their average body size (μm) commonly used in community ecology studies, a habitat trait (i.e., littoral, pelagic/littoral or pelagic) and a feeding trait (i.e., carnivorous, omnivorous, herbivorous or primary producer) referenced in species inventories. Animal species were then clustered to the family level (S = 48) and vegetal species were clustered to the class level (S = 10). This taxonomic aggregation led to 58 species clusters (hereafter called SC; **Supplementary Table 1**) gathered according to similar ecological functions/requirements and could hence be considered as functional nodes in the reconstructed food webs (Allesina and Pascual, 2009). This clustering procedure allowed to avoid unnecessary food web complexity by taking into account the main SC that may be directly or indirectly impacted by catfish in line with recommendations emerging from recent ecosystem modeling studies (Geary et al., 2020), to promote the computational efficiency and to facilitate ecological interpretations of the processes involved in abundance changes of SC due to *S. glanis*.

Allometric niche model and *silurus glanis* body size selection

We used the aNM (Vagnon et al., 2021) to infer trophic interactions between SC included in the typical peri-Alpine lake food web and to reconstruct the "non-invaded" (i.e., without *S. glanis*) and "invaded" food webs (i.e., with *S. glanis*). This model relies on the niche model principles (Williams and Martinez, 2000) stating that the niche position of consumer j is given by its average body size bs_j and that its resources fall within a body size range bs_r_j centered on bs_c_j. The range bounds were estimated using quantile regressions (i.e., bs_r_{jmin} = QR at 5% and bs_r_{jmax} = QR at 95%) as suggested by Gravel et al. (2013) and are specifically fitted whether consumers are vertebrate or invertebrate (Vagnon et al., 2021).

The aNM allowed obtaining a binary squared matrix (M_b) of trophic link occurrences of the whole food webs. These links were then weighted for each consumer j considering a Gaussian probability density function, similarly to Williams et al. (2010), with $\mu_j = bs\_c_j$ and σ_j = standard deviation of 100 points evenly spaced over bs_r_j (i.e., scaling of the normal distribution to bs_r_j). Weighted links were then normalized by the maximum value of the normal distribution to obtain a maximum weighting (0.95) at bs_c_j and a minimal weighting (0.1) corresponding to prey SC with body sizes at bs_r_j bounds. The resulting weighted links were finally converted as the proportion of resources i in the diet of consumer j (ω_{ji}, eq. 1), so that the total proportion of species in the diet of consumer j sums to 1.

$$\omega_{ji} = \frac{\text{Weighted Link}_{ji}}{\sum_{i\in\text{resources of } j}\text{Weighted Link}_{ji}} \qquad (1)$$

In a first step, trophic interactions between SC were first inferred without *S. glanis* to reconstruct the food web before invasion. Trophic positions (TP) of resident species were estimated according to the method of Levine (1980) with $TP_{Primaryproducers} = 1$ and $TP_{Consumers} = 1 + \text{mean}\ (TP_{Resources})$.

In a second step, we independently introduced 40 nodes representing *S. glanis* with increasing body sizes (i.e., 5–200 cm by 5 cm) in the SC inventory to study changes in the food web topology as *S. glanis* could cause different impacts due to its size-dependent diet (i.e., ontogenetic diet shift from invertebrates to fish; Carol et al., 2009; Copp et al., 2009; Alp, 2017). The directed connectance (i.e., number of actual links over the number of possible links) of each invaded food web was calculated to provide an estimate of interaction variations among resident species and *S. glanis* of different body sizes (**Supplementary Figure 1**; Bersier et al., 2002). Three body sizes associated with the highest variations of the directed connectance were selected to simulate three invasion scenarios: small body size 40 cm (S40), medium body size 85 cm (S85) and large body size 150 cm (S150). The trophic interactions inferred for the corresponding three invaded food webs were included in the following steps of the analysis.

Population dynamic model

The simulations of population dynamics were based on an updated version of the allometric population dynamic model proposed by Yodzis and Innes (1992) and extended by Brose et al. (2006). The dynamics of each primary producer i are given by:

$$\frac{dN_i}{dt} = r_i \cdot \left(1 - \frac{N_i}{K_i}\right) \cdot N_i - \sum_{j\in\text{consumers of i}} F_{ji}\left(\overrightarrow{N}\right) \cdot N_j \qquad (2)$$

The parameters are the intrinsic growth rate r_i and biotic capacity K_i. Both are allometrically scaled (**Supplementary Table 2**) differently from the ones proposed by Brose et al. The functional response (i.e., the *per capita* consumption rate of consumer j on resource i), $F_{ji}\left(\overrightarrow{N}\right)$ follows a Holling Type II and is given by:

$$F_{ji}\left(\overrightarrow{N}\right) = \frac{x_j \cdot y_j \cdot \omega_{ji} \cdot N_i}{1 + \sum_{k\,\epsilon\,\text{resource of } j} h_{jk} \cdot x_j \cdot y_j \cdot \omega_{jk} \cdot N_k} \qquad (3)$$

The parameters are x_j, the metabolic rate body mass dependent, and y_j the maximum consumption rate relative to the metabolic rate of consumer j. The former is newly allometrically scaled, while the latter depends on characteristic of the species

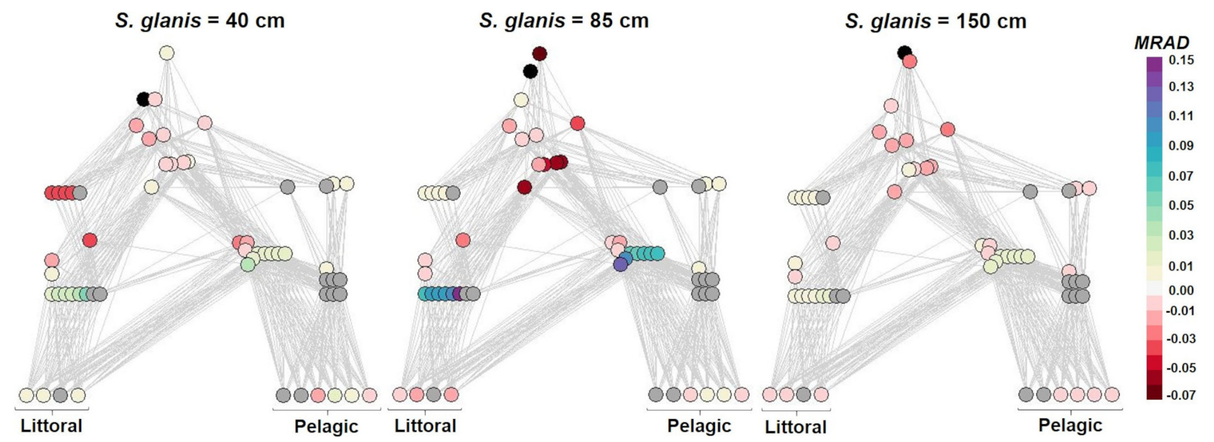

FIGURE 1

Effects of *S. glanis* throughout the whole invaded food-web typical of large French peri-Alpine lakes including independently *S. glanis* measuring 40, 85, and 150 cm. Nodes represent species clusters (SC) vertically arranged by increasing trophic position (*TP*) and colored according to the median value of the relative abundance differences (*MRAD)* used as an impact metric. Extinct species clusters are represented in dark gray and *S. glanis* is in black. The x-axis is defined as the gradient of pelagic reliance calculated from the initial pelagic reliance of primary producers set at 0 for littoral SC and 1 for the strict pelagic. The pelagic reliance of consumers was calculated by averaging the pelagic reliance of their resources considering ascending *TP*. When consumers shared the same *TP* and the same pelagic reliance, a delta of 0.02 was added to the pelagic reliance of the involved SC to avoid node overlapping in the plot.

(**Supplementary Table 2**). ω_{ji} is the proportion of resource i in the diet of consumer j (eq. 1) obtained from the weighting procedure previously described. The handling time h_{jk} of consumer j (i.e., time for handling and consuming the resource k) is also allometrically scaled (**Supplementary Table 2**), differently from the parameterization of Brose et al. for providing realistic estimations of this parameter. Finally, the dynamics of consumer j is given by:

$$\frac{dN_j}{dt} = -m_j \cdot N_j + \varepsilon_j \sum_{i \in \text{resources of } j} F_{ji}\left(\vec{N}\right) \cdot N_j - \sum_{l \in \text{consumers of } j} F_{lj}\left(\vec{N}\right) \cdot N_l \qquad (4)$$

The parameters are the morality rate m_j (allometrically scaled) and the consumption efficiency ε_j. (depends on species characteristics; **Supplementary Table 2**). Note that we choose N_i and N_j as the SC abundances (number of individuals in the SC) and not as the biomass for more stable calculations. Therefore, all allometrically scaled parameters are per individual (see **Supplementary Table 2**).

Simulations

We used 200 simulations of 20,000 time steps for all scenarios (no. *S. glanis*, S40, S85, and S150) and final results were obtained by averaging simulation outputs at each time step for each SC. Variability in metabolic rates was included in calculations by generating white noise following $\mathcal{N}$ ($\mu = 0$, $\sigma^2 = 0.1\%$ of metabolic rate). For each simulation, random initial abundances (N_0) were assumed to be uniformly distributed (Brose et al., 2006) on the interval [0.15–1] and were ranked according to average body sizes of SC (i.e., SC with the largest body size had the lower N0; Peters and Wassenberg, 1983). N_0 of *S. glanis* was fixed at 0.1 in all simulations to be lower than N_0 of the resident apex predator SC (Esocidae), to avoid bias resulting from the initial abundance variations of *S. glanis*.

Quantitative impacts

The impacts of *S. glanis* on resident species were investigated through two main ecological processes that are SC extinctions and changes in non-extinct SC abundance. Extinctions were assumed to be effective when the abundance of a SC fell below 1.10^{-6} (Ovaskainen and Hanski, 2003) and extinct SC were not permitted to reintegrate the system. Extinctions were explored both qualitatively (i.e., SC taxonomic category) and quantitatively (i.e., number of extinctions and time lags between time at extinction with and without *S. glanis*).

The impacts on the abundances of non-extinct SC were investigated by calculating the relative abundance difference (*RAD*; Eq. 5) at each time step to describe increase/decrease in abundances with *S. glanis* compared to abundances without *S. glanis* similarly to Zhang et al. (2019).

$$RAD = \frac{\text{Abundances with } S.\ glanis - \text{Abundances without } S.\ glanis}{\text{Abundances without } S.\ glanis} \qquad (5)$$

The median *RAD* (*MRAD*) for the 200 simulations was used to quantify the extent (i.e., amplitude of changes) as well as the type (positive, *MRAD* > 0, or negative, *MRAD* < 0) of *S. glanis* impact on SC abundances (i.e., increase or decrease in abundances).

The model robustness was assessed by including an increasing variability in the metabolic rate using white noise (i.e., $\mathcal{N}$ (μ = 0, σ^2 = 0.1, 0.5, 1, 5, 10, and 20%; **Supplementary Figures 3–9**) using MRAD as the response variable.

Ecological interactions

Impacts of *S. glanis* on SC (extinct or with modified abundances) were classified according to three main ecological interactions based on the food web structure inferred with the aNM:

(i) Predation when a SC was a prey for *S. glanis;*

(ii) Competition when a SC shared common resources but did not directly interact with *S. glanis*. In this case, Schoener's overlap index was complementarily calculated to quantify diet similarities between both competitors (Vera-Duarte and Landaeta, 2017) as follows:

$$Schoener's\ index = 1 - 0.5 \sum_{i} \left| P_{xi} - P_{yi} \right| \qquad (6)$$

where P_{xi} and P_{yi} are the proportions of resource *i* in the inferred diet of competitor *x* and *y;*

(iii) Trophic cascades were considered when a SC was not a prey of *S. glanis* and corresponded to repercussions across multiple trophic levels (Carpenter et al., 2010).

Interactions not corresponding to these three ecological interactions were classified as "Others."

All statistical and graphical displays were performed using R.3.5.1 (R Core Team, 2018) with the packages ade4 (Dray and Dufour, 2007), deSolve (Soetaert et al., 2010), cheddar (Hudson et al., 2013), igraph (Csárdi, 2019), NetIndices (Kones et al., 2009), foodweb (Perdomo, 2015), ggplot2 (Wickham, 2016). R Markdown files with data and R codes summarizing the conducted analyses are available at https://github.com/chloevagnon/aNM-and-population-dynamics to provide reproducible examples.

Results

General impacts of *silurus glanis* within the whole food web

Extinctions did not relate to *S. glanis* body sizes as the same extinctions occurred for the three different invasion scenarios (**Figure 1**). Extinct species clusters (SC) corresponded to different trophic levels (from primary producers to secondary consumers) and were mainly characterized by a high pelagic reliance (**Supplementary Figure 11**). In contrast, *S. glanis* body size was determinant in the amplitude of abundance changes of the non-extinct SC (i.e., *MRAD* from –0.07 to +0.15). The strongest negative impacts were found for SC with *TP* (Trophic Position) close to the invader's *TP* in the food webs while positive impacts mainly concerned SC with low *TP* (**Figure 1**). The lowest and the highest *MRAD* were observed for S85 and suggested positive impacts on primary littoral and pelagic consumers, and negative ones on SC with *TP* > 2.5 (**Figure 1**). Littoral secondary consumers were mainly impacted for S40 and the lowest *MRAD* were found for S150.

Extinction patterns

Among the 58 SC, 14 were extinct at the end of the simulations in each scenario (**Figure 2A**). Three major extinction phases were noticeable and concerned in the first place zooplankton (up to 1,043.3 ± 0.5 time steps), followed by invertebrates and phytoplankton (up to 10,475.8 ± 4.3 time steps), and finally one invertebrate (at 17,915.5 ± 35.2 time steps). The same extinctions patterns occurred for all scenarios while time lags between extinctions differed, particularly for the latest extinctions (**Figure 2B**). Extinctions tented to occur earlier for S85 and S150 while those could appear later for S40 compared to extinctions without *S. glanis*.

Abundance changes

RAD (Relative Abundance Differences) varied among SC taxonomic categories and for the different *S. glanis* body sizes. Fish SC were impacted for all scenarios while presenting variable changes as shown by the boxplots representing *RAD* at each time step (**Figure 3A**). The three smallest fish SC and the largest one were especially negatively impacted by S85 (lowest *RAD* and highest variability), followed by S150 especially for the largest fish SC. In contrast, negative effects of S40 were more pronounced for medium-size fish SC and even appeared positive for two fish SC.

Half of invertebrate SC had higher abundances in presence of all *S. glanis* and presented a high variability along time steps, particularly with S85 (i.e., highest *RAD*; **Figure 3B**). The other half of invertebrate SC was negatively impacted by S40 for all time steps (i.e., all RAD values < 0) and the three largest invertebrates were negatively affected by S85 and S150.

RAD for phytoplankton, phytobenthos and zooplankton SC were similar among scenarios and more variable in time for phytobenthos SC (**Figure 3C**). Abundances of zooplankton and phytobenthos SC slightly increased for S40 while they decreased in the scenarios with the two larger *S. glanis* (S85 and S150). Abundances of half of phytoplankton SC increased with *S. glanis* body size while the reverse was found for the other half of phytoplankton SC.

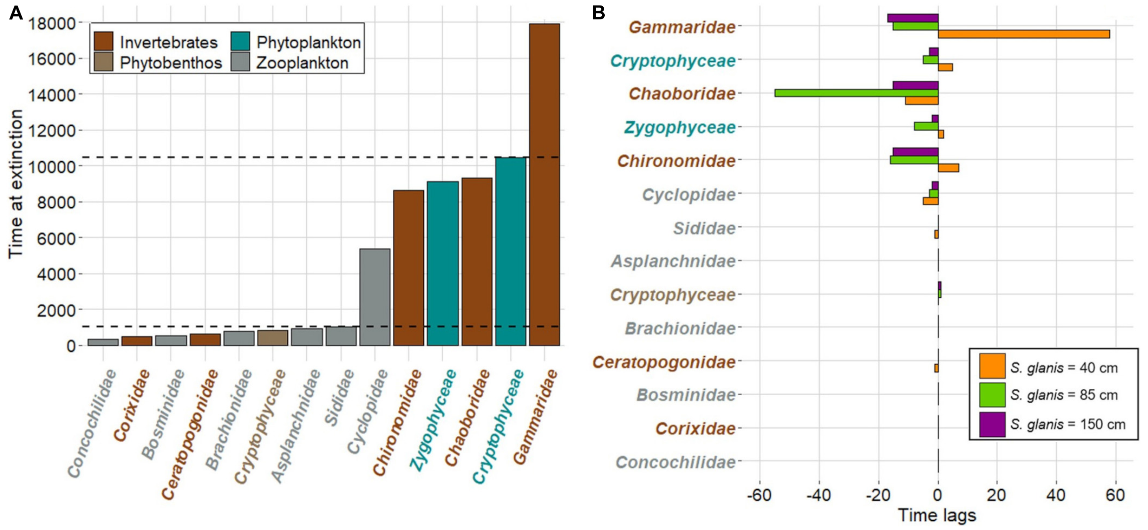

FIGURE 2
Extinctions of species clusters (SC) in the whole invaded food-web typical of large French peri-Alpine lakes including independently *S. glanis* measuring 40, 85, and 150 cm. **(A)** Time at extinction over the 20,000 time steps for the SC are represented (three major extinction phases are delineated by horizontal dashed lines) and correspond to all scenarios. **(B)** Time lags between time at extinction associated with *S. glanis* invasion are represented according to the different invasion scenarios. SC are ordered by decreasing time at extinction (from top to bottom). Negative and positive time lags indicate extinctions occurring earlier and latter than without *S. glanis* invasion, respectively.

Ecological interactions

Extinctions may have been caused by trophic cascades regarding the low trophic position of extinct SC compared to that of the three *S. glanis*, even for one invertebrate SC predated by S40 (**Figure 4A** and **Supplementary Table 3**), but did not seem directly triggered by *S. glanis* as they also occurred without the predator in the food web.

Ecological interactions for non-extinct SC were much more diverse among scenarios and corresponded to both negative and positive impacts mediated by direct and indirect interactions, even for three interactions with fish SC for S40 and S85 (**Figure 4B** and **Supplementary Table 3**).

Direct negative impacts corresponded to predation with 13 SC for S40 (91% of invertebrate SC), seven SC for S85 (large invertebrates and medium-size fish SC) and 10 SC for S150 (crayfish and all fish SC).

Indirect negative impacts were emphasized through competition identified for different fish SC when considering the invasion of S40 (e.g., Lotidae, Cyprinidae, Ictaluridae; Schoener's index of 0.78, 0.54 and 0.53, respectively), S85 (e.g., Esocidae; Schoener's index = 0.91) and S150 (Esocidae; Schoener's index = 0.71). Negative impacts were also due to trophic cascades, concerning three SC for S40 and increasing with *S. glanis* body size (i.e., 10 SC for S85 and 14 SC for S150).

Among the different ecological interactions, Indirect positive interactions were preponderant with 21 trophic cascades identified for S40 (composed at 67% of invertebrate SC, 5% of zooplankton and 28% of primary producer SC), 22 trophic cascades for S85 (composed of 82% of invertebrate SC, 9% of zooplankton and 9% of primary producer SC) and 19 trophic cascades for S150 (100 % of invertebrate SC).

Sensitivity analysis

The sensitivity analysis revealed a gradual increase in *MRAD* variability in response to the increasing metabolic noise. However, *MRAD* distribution remained consistent among scenarios and SC categories for metabolic noise up to 5% and then started to flatten, traducing a decrease in the consistency of the results with higher metabolic noises (**Supplementary Figures 3–9**). Especially fish SC seemed more sensitive than other SC to metabolic noise. Therefore, our simulations could be sensitive to high metabolic rate variability while patterns in responses remained robust according to taxonomic categories and among the invasion scenarios.

Discussion

Our approach combines trophic interaction inferences from the aNM with a dynamic population model allowing a thorough investigation of an invasive species impacts at the whole lake food web scale. It supported the consideration of direct and indirect interactions between residents and the invader and thus investigation of both positive and negative impacts on their abundances.

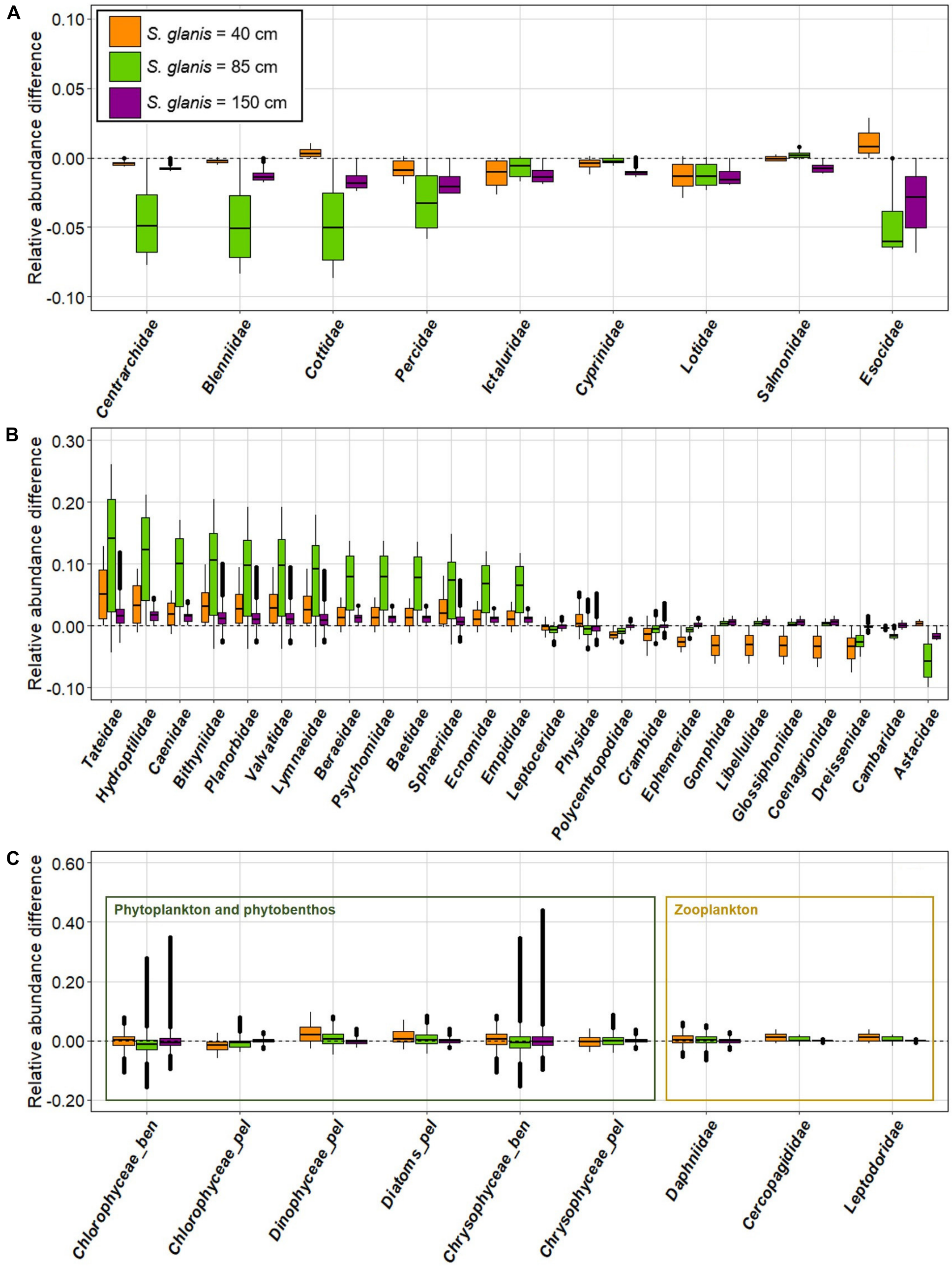

FIGURE 3

Relative abundance differences (RAD) along the 20,000 time steps for each invasion scenario providing the effect of *S. glanis* on the species clusters of fish **(A)**, invertebrate **(B)** and primary producers and zooplankton **(C)** in the whole invaded food-web typical of large French peri-Alpine lakes. Species clusters are ordered by increasing body sizes from left to right. Boxes comprise 25–75% quantiles and horizontal full lines indicate median values. Median values below 0 correspond to an overall abundance depletion following *S. glanis* invasion while median values above 0 correspond to an abundance increase.

A new predator in peri-alpine lake food webs

The food web topology was only slightly modified by the invasion of *S. glanis*, which exerted moderate impacts on connectance and abundance modifications (i.e., low connectance changes and restrained amplitude of abundance modifications). This result may be explained by the rather high resolution of the food web, as associated to omnivory that both promote weak interaction strengths (**Supplementary Table 4**) and stability in the persistence of communities (Emmerson and Yearsley, 2004; Dunne et al., 2005; Landi et al., 2018;

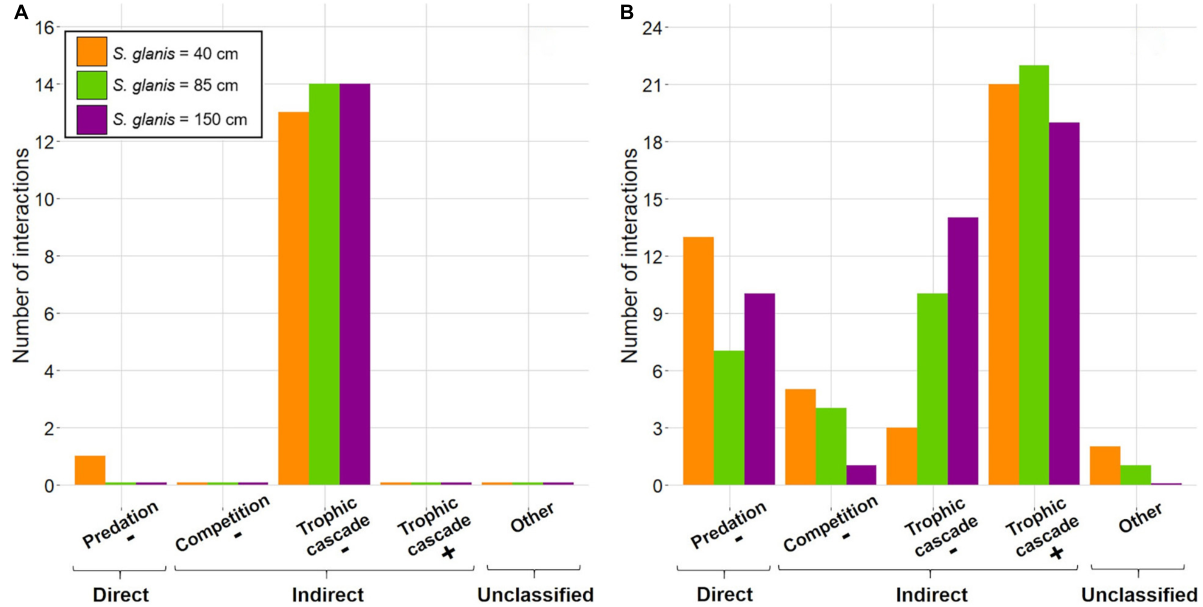

FIGURE 4
Ecological interactions involved in time lags for extinct species clusters **(A)** and for species clusters submitted to abundances changes **(B)** in the whole invaded food-web typical of large French peri-Alpine lakes. The "−" corresponds to interactions with negative impacts on species cluster abundances (i.e., *MRAD* < 0). Contrary, "+" is used for interactions with positive impacts on species clusters abundances (i.e., *MRAD* > 0).

Kawatsu et al., 2021). Ecological interactions and abundance dynamics were nevertheless influenced by *S. glanis* and were modulated according to its body size.

The highest negative impacts of *S. glanis* were related to direct interactions for resources acquisition. Predation was indeed the main ecological interaction associated with the decrease in SC abundances, in lines with numerous impact studies on invasive fish (Gozlan et al., 2010; Van der Veer and Nentwig, 2015; David et al., 2017). Specifically, the decrease in abundance of invertebrate SC (e.g., Ephemeridae) and small fish SC (e.g., Blenniidae) would be caused by *S. glanis* of 40 cm while the decrease of larger fish SC (e.g., Percidae) and large invertebrate SC (e.g., crayfish) would mostly result from the invasion of larger *S. glanis* (85 cm and 150 cm). Percidae and crayfish represented consistent fraction of *S. glanis* diet in empirical studies (Carol et al., 2009; Ferreira et al., 2019) and the presence of *S. glanis* was suspected to alter their abundance in few ecosystems (Copp et al., 2009; Guillerault et al., 2015; Vagnon et al., 2022), suggesting plausible predictions from our approach. Competition between *S. glanis* and large fish SC was also suggested to negatively alter fish abundances and particularly dampened the abundance of the resident apex predator (Esocidae; high diet overlaps for S85 and S150) while fish SC with weak diet overlaps (Schoener index < 0.1) were poorly or not impacted. These results supported both plausible inferences of trophic interactions for predators and species abundance alterations due to both predation and competition. Indeed, invasive predators frequently cause decreases in abundances of their prey (Mills et al., 2004; David et al., 2017), they are expected to have a strong competitive effect in aquatic ecosystems and they are known to induce changes in species assemblages (Gozlan et al., 2010; Allesina and Tang, 2012; David et al., 2017).

Interestingly our results highlighted that considering two trophic levels (i.e., consumer/resource) or two competitors does not allow to identify major impacts of invasive species and their repercussions at the whole food web scale as we underlined main abundance changes for SC through trophic cascades, and particularly we found higher positive impacts than negative ones. A succession of negative and positive impacts was indeed noticeable along the food web and emphasized typical patterns of top-down cascades found in aquatic ecosystems (Carpenter et al., 2010; Heath et al., 2014; Su et al., 2021). In these processes, the negative impacts on abundances of SC such as fish result in a relaxed predation on lower trophic levels (e.g., grazers) and thus in a reduction of primary producers (Carpenter et al., 2008; Heath et al., 2014; Koning and McIntyre, 2021). Consequently, positive and negative impacts were higher for S85 than for S40 and S150, as fish and large invertebrate SC were particularly impacted in this invasion scenario (i.e., competition with fish SC and predation on both fish and large invertebrate SC). Complementarily, trophic cascades were suggested to modulate time at extinctions (earlier for S85 and S150 and later for S40), yet the presence of *S. glanis* did not qualitatively influence extinction processes (i.e., same extinctions with/without *S. glanis*). These results underline the ability of *S. glanis* to cause top-down trophic cascades by regulating mesopredator abundances while suggesting that it may not be a major source of species extinctions, similarly to empirical studies conducted in reservoirs, lakes and rivers (Copp et al., 2009; Vejřík et al., 2017). In fact, the opportunistic feeding behavior of *S. glanis* (Copp et al., 2009; Cucherousset et al., 2018; Vagnon et al., 2022) could foster its reliance on a diversified prey set limiting strong interaction strengths usually known to induce stronger impacts on resident species populations than weak interactions (Terraube et al., 2011; Wootton and Stouffer, 2016).

Model limits and strengths

Our study based on the combination of an allometric niche model and an alternative version of the population dynamic model of Brose et al. (2006) succeeded at supporting a comprehensive assessment of resident species abundance modifications and the involved trophic interactions considering a multi-trophic system, often challenging to evaluate only based on experiments or on traditional empirical methods (Crystal-Ornelas and Lockwood, 2020), notwithstanding process simplifications inherent to the elaborated method and to our study objectives.

Firstly, we considered an average body size to represent species nodes in food webs and we integrated independently a unique *S. glanis* body size node in simulation scenarios. While we recognize that diets of both resident and *S. glanis* populations can be ontogenetic-dependent, we conserved this approach commonly approved in community ecology to preserve the real significance of each node in the food web (i.e., one *S. glanis* node = one invertebrate node = one phytoplankton node). Secondly, we assumed environmental and anthropic drivers constant to capture specifically the invasive species impacts in the recipient ecosystem. Although these factors are known to be dynamic in real systems (Brose and Hillebrand, 2016), our approach appeared relevant considering the different time scales involved in species abundances modifications following exposure to various external pressures. Indeed, the catfish impacts could be observed more rapidly than external factors such as climate change (i.e., decades vs. several decades). Our dynamic model could obviously be completed in future studies to account for possible other drivers of species trophic interactions and their dynamics (e.g., metabolism modifications following temperature increase due to climate change) but remained out of the scope of this study.

However, the combination of allometric models would be appropriate for an application to a broad aquatic ecosystem array where body size governs trophic interactions, mainly thanks to the minimal required data inputs often available from monitoring surveys or literature (i.e., species inventory and the average species body sizes). Here we used species clusters for convenience and for limiting computation concerns such as singularities but different taxonomic resolutions can be considered depending on the initial study scope. Moreover, allometric parameterizations in the dynamic model could also be replaced by empirical data (e.g., body mass, metabolic rate) and/or can be completed by other calculation methods, for instance, to infer interaction strengths between consumers and resources (Calizza et al., 2021). When these data are not available, our initial simulation parameterization appears valuable regarding the convergence between our results and literature on predator impacts in food webs and freshwater ecosystems (Cucherousset and Olden, 2011; Cucherousset et al., 2012; Jackson et al., 2017), although empirical validations of our simulations still remain out of reach. Indeed, management plans mostly focus on a part of species compared to the totality of resident species to survey, mainly due to the restricted resources available for management actions (Vander Zanden and Olden, 2008), thus limiting the consideration of all taxa responses at long term that could be underlined in our study.

Overall, our study framework addresses the impact of invasive species and may be relevant regarding the increasing rate of species introductions representing a major threat to ecosystems (Lockwood et al., 2013). We underlined the importance of considering interspecific interactions at the whole food web scale for the assessment of invasive species impacts. The introduction of invaders indeed frequently involves a wide diversity of new ecological interactions, resulting in modifications of species abundances through both direct and indirect interactions and thus causing non-negligible impacts on resident communities. The balance between negative and positive aspects of invasions is also a significant factor to consider as positive effects of invasions can appear non-negligible, and may attenuate *a priori* expectations (Gozlan, 2008; Tablado et al., 2010; Schlaepfer et al., 2011). Our study can thus participate to the growing corpus of methodologies trying to reach comprehensive assessments and predictions of invader impacts, considering their direct/indirect and positive/negative effects in freshwater ecosystems.

Data availability statement

The original contributions presented in this study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

Author contributions

CV, RPR, L-FB, FC, JG, and VF designed the study. CV led data analyses and manuscript writing with RPR and VF. All authors provided critical feedbacks.

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Conflict of interest

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.913954/full#supplementary-material

References

Albertson, L. K., MacDonald, M. J., Tumolo, B. B., Briggs, M. A., Maguire, Z., Quinn, S., et al. (2021). Uncovering patterns of freshwater positive interactions using meta-analysis: identifying the roles of common participants, invasive species and environmental context. *Ecol. Lett.* 24, 594–607. doi: 10.1111/ele.13664

Alexander, M. E., Dick, J. T. A., and O'Connor, N. E. (2013). Trait-mediated indirect interactions in a marine intertidal system as quantified by functional responses. *Oikos* 122, 1521–1531.

Allesina, S., and Pascual, M. (2009). Food web models: a plea for groups. *Ecol. Lett.* 12, 652–662. doi: 10.1111/j.1461-0248.2009.01321.x

Allesina, S., and Tang, S. (2012). Stability criteria for complex ecosystems. *Nature* 483, 205–208.

Alp, A. (2017). Diet shift and prey selection of the native European catfish, *Silurus glanis*, in a Turkish reservoir. *J. Limnol. Freshw. Fish. Res.* 3, 15–23. doi: 10.17216/limnofish.288217

Barrios-O'Neill, D., Dick, J. T., Emmerson, M. C., Ricciardi, A., MacIsaac, H. J., Alexander, M. E., et al. (2014). Fortune favours the bold: a higher predator reduces the impact of a native but not an invasive intermediate predator. *J. Anim. Ecol.* 83, 693–701. doi: 10.1111/1365-2656.12155

Bersier, L. F., Banasek-Richter, C., and Cattin, M. C. (2002). Quantitative descriptors of food-web matrices. *Ecology* 83, 2394–2407.

Brose, U., and Hillebrand, H. (2016). Biodiversity and ecosystem functioning in dynamic landscapes. *Philos. Trans. R. Soc. B* 371:20150267.

Brose, U., Williams, R. J., and Martinez, N. D. (2006). Allometric scaling enhances stability in complex food webs. *Ecol. Lett.* 9, 1228–1236. doi: 10.1111/j.1461-0248.2006.00978.x

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., and West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology* 85, 1771–1789.

Brucet, S., Tavşanoğlu, ÜN., Özen, A., Levi, E. E., Bezirci, G., Çakıroğlu, A. İ, et al. (2017). Size-based interactions across trophic levels in food webs of shallow Mediterranean lakes. *Freshw. Biol.* 62, 1819–1830. doi: 10.1111/fwb.12997

Calizza, E., Rossi, L., Careddu, G., Sporta Caputi, S., and Costantini, M. L. (2021). A novel approach to quantifying trophic interaction strengths and impact of invasive species in food webs. *Biol. Invasions* 23, 2093–2107. doi: 10.1007/s10530-021-02490-y

Carol, J., Benejam, L., Benito, J., and García-Berthou, E. (2009). Growth and diet of European catfish (*Silurus glanis*) in early and late invasion stages. *Fundam. Appl. Limnol.* 174, 317–328. doi: 10.1127/1863-9135/2009/0174-0317

Carpenter, S., Brock, W., Cole, J., Kitchell, J., and Pace, M. (2008). Leading indicators of trophic cascades. *Ecol. Lett.* 11, 128–138.

Carpenter, S., Cole, J., Kitchell, J., and Pace, M. (2010). "Chapter 4. Trophic Cascades in Lakes: Lessons and Prospects," in *Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature*, eds J. Terborgh and J. A. Este (Washington D.C: Island Press).

Copp, G. H., Robert Britton, J., Cucherousset, J., García-Berthou, E., Kirk, R., Peeler, E., et al. (2009). Voracious invader or benign feline? A review of the environmental biology of European catfish *Silurus glanis* in its native and introduced ranges. *Fish Fish.* 10, 252–282. doi: 10.1111/j.1467-2979.2008.00321.x

Crystal-Ornelas, R., and Lockwood, J. L. (2020). The 'known unknowns' of invasive species impact measurement. *Biol. Invasions* 22, 1513–1525. doi: 10.1007/s10530-020-02200-0

Csárdi, G. (2019). *Package 'igraph'. R-Project Version 0.8.1.*

Cucherousset, J., and Olden, J. (2011). Ecological Impacts of Non-native Freshwater Fishes. *Fisheries* 36, 215–230.

Cucherousset, J., Bouletreau, S., Martino, A., Roussel, J. M., and Santoul, F. (2012). Using stable isotope analyses to determine the ecological effects of non-native fishes. *Fish. Manag. Ecol.* 19, 111–119. doi: 10.1111/j.1365-2400.2011.00824.x

Cucherousset, J., Horky, P., Slavík, O., Ovidio, M., Arlinghaus, R., Boulêtreau, S., et al. (2018). Ecology, behaviour and management of the European catfish. *Rev. Fish Biol. Fish.* 28, 177–190. doi: 10.1007/s11160-017-9507-9

Cuthbert, R. N., Dalu, T., Wasserman, R. J., Dick, J. T. A., Mofu, L., Callaghan, A., et al. (2018). Intermediate predator naivete and sex-skewed vulnerability predict the impact of an invasive higher predator. *Sci. Rep.* 8:14282. doi: 10.1038/s41598-018-32728-0

Cuthbert, R. N., Dickey, J. W. E., Coughlan, N. E., Joyce, P. W. S., and Dick, J. T. A. (2019). The Functional Response Ratio (FRR): advancing comparative metrics for predicting the ecological impacts of invasive alien species. *Biol. Invasions* 21, 2543–2547. doi: 10.1007/s10530-019-02002-z

David, P., Thébault, E., Anneville, O., Duyck, P. F., Chapuis, E., and Loeuille, N. (2017). "Impacts of Invasive Species on Food Webs," in *Networks of Invasion: A Synthesis of Concepts*, eds D. Bohan, A. Dumbrell, and F. Massol (Cambridge: Academic Press), 1–60.

Diagne, C., Leroy, B., Gozlan, R. E., Vaissiere, A. C., Assailly, C., Nuninger, L., et al. (2020). InvaCost, a public database of the economic costs of biological invasions worldwide. *Sci. Data* 7:277. doi: 10.1038/s41597-020-00586-z

Dick, J. T. A., Alexander, M. E., Jeschke, J. M., Ricciardi, A., MacIsaac, H. J., Robinson, T. B., et al. (2014). Advancing impact prediction and hypothesis testing in invasion ecology using a comparative functional response approach. *Biol. Invasions* 16, 735–753. doi: 10.1007/s10530-013-0550-8

Dick, J. T. A., Laverty, C., Lennon, J. J., Barrios-O'Neill, D., Mensink, P. J., Robert Britton, J., et al. (2017). Invader Relative Impact Potential: a new metric to understand and predict the ecological impacts of existing, emerging and future invasive alien species. *J. Appl. Ecol.* 54, 1259–1267. doi: 10.1111/1365-2664.12849

Dickey, J. W. E., Cuthbert, R. N., Rea, M., Laverty, C., Crane, K., South, J., et al. (2018). Assessing the relative potential ecological impacts and invasion risks of emerging and future invasive alien species. *NeoBiota* 40, 1–24. doi: 10.3897/neobiota.40.28519

Dray, S., and Dufour, A. B. (2007). The ade4 package: implementing the duality diagram for ecologists. *J. Stat. Softw.* 22, 1–20.

Dunne, J. A., Brose, U., Williams, R. J., and Martinez, N. D. (2005). "Modeling food-web dynamics: complexity–stability implications," in *Aquatic Food Webs: An Ecosystem Approach*, eds A. Belgrano, U. M. Scharler, J. Dunne, and R. E. Ulanowicz (Oxford: Oxford Univeristy Press), 117–129.

Emmerson, M., and Yearsley, J. M. (2004). Weak interactions, omnivory and emergent food-web properties. *Proc. R. Soc. B: Biol. Sci.* 271, 397–405. doi: 10.1098/rspb.2003.2592

Ferreira, M., Gago, J., and Ribeiro, F. (2019). Diet of European catfish in a newly invaded region. *Fishes* 4:58. doi: 10.3390/fishes4040058

Frost, C. M., Allen, W. J., Courchamp, F., Jeschke, J. M., Saul, W. C., and Wardle, D. A. (2019). Using Network Theory to Understand and Predict Biological Invasions. *Trends Ecol. Evol.* 34, 831–843. doi: 10.1016/j.tree.2019.04.012

Geary, W. L., Bode, M., Doherty, T. S., Fulton, E. A., Nimmo, D. G., Tulloch, A. I. T., et al. (2020). A guide to ecosystem models and their environmental applications. *Nat. Ecol. Evol.* 4, 1459–1471. doi: 10.1038/s41559-020-01298-8

Gozlan, R. E. (2008). Introduction of non-native freshwater fish: is it all bad? *Fish Fish.* 9, 106–115. doi: 10.1111/j.1467-2979.2007.00267.x

Gozlan, R. E., Britton, J. R., Cowx, I., and Copp, G. H. (2010). Current knowledge on non-native freshwater fish introductions. *J. Fish Biol.* 76, 751–786. doi: 10.1111/j.1095-8649.2010.02566.x

Gravel, D., Poisot, T., Albouy, C., Velez, L., Mouillot, D., and Freckleton, R. (2013). Inferring food web structure from predator-prey body size relationships. *Methods Ecol. Evol.* 4, 1083–1090. doi: 10.1111/2041-210x.12103

Guillerault, N., Delmotte, S., Boulêtreau, S., Lauzeral, C., Poulet, N., and Santoul, F. (2015). Does the non-native European catfish Silurus glanis threaten French river fish populations? *Freshw. Biol.* 60, 922–928. doi: 10.1111/fwb.12545

Heath, M. R., Speirs, D. C., and Steele, J. H. (2014). Understanding patterns and processes in models of trophic cascades. *Ecol. Lett.* 17, 101–114.

Hudson, L. N., Emerson, R., Jenkins, G. B., Layer, K., Ledger, M. E., Pichler, D. E., et al. (2013). Cheddar: analysis and visualisation of ecological communities in R. *Methods Ecol. Evol.* 4, 99–104. doi: 10.1111/2041-210x.12005

Jackson, M. C., Wasserman, R. J., Grey, J., Ricciardi, A., Dick, J. T. A., and Alexander, M. E. (2017). "Novel and Disrupted Trophic Links Following Invasion in Freshwater Ecosystems," in *Networks of Invasion: Empirical Evidence and Case Studies*, eds D. Bohan, A. Dumbrell, and F. Massol (Cambridge: Academic Press), 55–97.

Jacquet, S., Domaizon, I., and Anneville, O. (2014). The need for ecological monitoring of freshwaters in a changing world: a case study of Lakes Annecy, Bourget, and Geneva. *Environ. Monit. Assess.* 186, 3455–3476. doi: 10.1007/s10661-014-3630-z

Kamenova, S., Bartley, T. J., Bohan, D. A., Boutain, J. R., Colautti, R. I., Domaizon, I., et al. (2017). "Invasions Toolkit : Current methods for tracking the spread and impact of invasive species," in *Networks of Invasion: A Synthesis of Concepts*, eds D. Bohan, A. Dumbrell, F. Massol, D. Bohan, A. Dumbrell, and F. Massol (Cambridge: Academic Press), 85–182.

Kawatsu, K., Ushio, M., van Veen, F. J. F., and Kondoh, M. (2021). Are networks of trophic interactions sufficient for understanding the dynamics of multi-trophic communities? Analysis of a tri-trophic insect food-web time-series. *Ecol. Lett.* 24, 543–552. doi: 10.1111/ele.13672

Kones, J. K., Soetaert, K., van Oevelen, D., and Owino, J. O. (2009). Are network indices robust indicators of food web functioning? A Monte Carlo approach. *Ecol. Model.* 220, 370–382. doi: 10.1016/j.ecolmodel.2008.10.012

Koning, A. A., and McIntyre, P. B. (2021). Grassroots reserves rescue a river food web from cascading impacts of overharvest. *Front. Ecol. Environ.* 19:152–158. doi: 10.1002/fee.2293

Landi, P., Minoarivelo, H. O., Brännström, Å, Hui, C., and Dieckmann, U. (2018). Complexity and stability of ecological networks: a review of the theory. *Popul. Ecol.* 60, 319–345. doi: 10.1007/s10144-018-0628-3

Levine, S. (1980). Several measures of trophic structure applicable to complex food webs. *J. Theor. Biol.* 83, 195–207. doi: 10.1007/s00442-014-2936-4

Lockwood, J. L., Hoopes, M. F., and Marchetti, M. P. (2013). *Invasion Ecology (Second Edition)*. Hoboken: Wiley–Blackwell.

Mills, M. D., Rader, R. B., and Belk, M. C. (2004). Complex interactions between native and invasive fish: the simultaneous effects of multiple negative interactions. *Oecologia* 141, 713–721. doi: 10.1007/s00442-004-1695-z

Ovaskainen, O., and Hanski, I. (2003). Extinction threshold in metapopulation models. *Ann. Zool. Fenn.* 40, 81–97.

Perdomo, G. (2015). *Package 'Foodweb'. Version 1.0*. Available Online at: https://CRAN.R-project.org/package=foodweb (accessed April 5, 2020).

Petchey, O. L., Beckerman, A. P., Riede, J. O., and Warren, P. H. (2008). Size, foraging, and food web structure. *Proc. Natl. Acad. Sci. U.S.A.* 105, 4191–4196.

Peters, R. H., and Wassenberg, K. (1983). The effect of body size on animal abundance. *Oecologia* 60, 89–96.

Pomeranz, J. P. F., Thompson, R. M., Poisot, T., Harding, J. S., and Lecomte, N. (2019). Inferring predator–prey interactions in food webs. *Methods Ecol. Evol.* 10, 356–367. doi: 10.1111/2041-210x.13125

R Core Team (2018). *R: A Language And Environment For Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Rimet, F., Anneville, O., Barbet, D., Chardon, C., Crépin, L., Domaizon, I., et al. (2020). The Observatory on LAkes (OLA) database: sixty years of environmental data accessible to the public. *J. Limnol.* 79, 164–178. doi: 10.4081/jlimnol.2020.1944

Schlaepfer, M., Sax, D., and Olden, J. (2011). The Potential Conservation Value of Non-Native Species. *Conserv. Biol.* 25, 428–437.

Shurin, J. B., Borer, E. T., Seabloom, E. W., Anderson, K., Blanchette, C. A., Broitman, B., et al. (2002). A cross-ecosystem comparison of the strength of trophic cascades. *Ecol. Lett.* 5, 785–791. doi: 10.1046/j.1461-0248.2002.00381.x

Soetaert, K., Petzoldt, T., and Setzer, W. R. (2010). Solving Differential Equations in R: package deSolve. *J. Stat. Softw.* 33, 1–25.

Su, H., Feng, Y., Chen, J., Chen, J., Ma, S., Fang, J., et al. (2021). Determinants of trophic cascade strength in freshwater ecosystems: a global analysis. *Ecology* 102:e03370. doi: 10.1002/ecy.3370

Tablado, Z., Tella, J. L., Sanchez-Zapata, J. A., and Hiraldo, F. (2010). The paradox of the long-term positive effects of a North American crayfish on a European community of predators. *Conserv. Biol.* 24, 1230–1238. doi: 10.1111/j.1523-1739.2010.01483.x

Terraube, J., Arroyo, B., Madders, M., and Mougeot, F. (2011). Diet specialisation and foraging efficiency under fluctuating vole abundance: a comparison between generalist and specialist avian predators. *Oikos* 120, 234–244.

Terry, J. C. D., Morris, R. J., and Bonsall, M. B. (2018). Trophic Interaction Modifications Disrupt The Structure and Stability of Food Webs. *bioRxiv* [Preprint] doi: 10.1101/345280

Vagnon, C., Bazin, S., Cattanéo, F., Goulon, C., Guillard, J., and Frossard, V. (2022). The opportunistic trophic behaviour of the European catfish (*Silurus glanis*) in a recently colonised large peri-alpine lake. *Ecol. Freshw. Fish* doi: 10.1111/eff.12659

Vagnon, C., Cattanéo, F., Goulon, C., Grimardias, D., Guillard, J., and Frossard, V. (2021). An allometric niche model for species interactions in temperate freshwater ecosystems. *Ecosphere* 12:e03420.

Van der Veer, G., and Nentwig, W. (2015). Environmental and economic impact assessment of alien and invasive fish species in Europe using the generic impact scoring system. *Ecol. Freshw. Fish* 24, 646–656. doi: 10.1111/eff.12181

Vander Zanden, M. J., and Olden, J. D. (2008). A management framework for preventing the secondary spread of aquatic invasive species. *Can. J. Fish. Aquat. Sci.* 65, 1512–1522.

Vejřík, L., Vejříková, I., Blabolil, P., Eloranta, A. P., Kočvara, L., Peterka, J., et al. (2017). European catfish (*Silurus glanis*) as a freshwater apex predator drives ecosystem *via* its diet adaptability. *Sci. Rep.* 7:15970. doi: 10.1038/s41598-017-16169-9

Vera-Duarte, J. A., and Landaeta, M. F. (2017). Feeding habits and dietary overlap during the larval development of two sandperches (Pisces: pinguipedidae). *Sci. Mar.* 81, 195–204. doi: 10.3989/scimar.04544.06A

Wickham, H. (2016). *Ggplot2: Elegant Graphics For Data Analysis*. New-York, NY: Springer-Verlag.

Williams, R. J., Anandanadesan, A., and Purves, D. (2010). The probabilistic niche model reveals the niche structure and role of body size in a complex food web. *PLoS One* 5:e12092. doi: 10.1371/journal.pone.0012092

Williams, R. J., and Martinez, N. D. (2000). Simple rules yield complex food webs. *Nature* 404, 180–183. doi: 10.1038/35004572

Wootton, K. L., and Stouffer, D. B. (2016). Many weak interactions and few strong; food-web feasibility depends on the combination of the strength of species' interactions and their correct arrangement. *Theor. Ecol.* 9, 185–195. doi: 10.1007/s12080-015-0279-3

Yodzis, P., and Innes, S. (1992). Body Size and Consumer-Resource Dynamics. .*Am. Nat.* 139, 1151–1175.

Zhang, H., Rutherford, E. S., Mason, D. M., Wittmann, M. E., Lodge, D. M., Zhu, X., et al. (2019). Modeling potential impacts of three benthic invasive species on the Lake Erie food web. *Biol. Invasions* 21, 1697–1719. doi: 10.1007/s10530-019-01929-7

Zhang, J., Qian, H., Girardello, M., Pellissier, V., Nielsen, S. E., and Svenning, J. C. (2018). Trophic interactions among vertebrate guilds and plants shape global patterns in species diversity. *Proc. Biol. Sci.* 285:20180949. doi: 10.1098/rspb.2018.0949

Supplementary material of:
Combining food-web theory and population dynamics to assess the impact of invasive species

R-code part 1: Inferences of trophic interactions

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June 2021

Function definition

Function 1: get_niche_attributes

Infer the niche attributes of species in the species inventory based on their body size and their category. Niche parameters of primary producers are automatically set at 0. The function requires the package “stringr”.

Input: Data are ordered by decreasing body sizes.

1. species_name = the name of the species to use
2. body_size = log10(vector of species body sizes in μm)
3. species_category = “vertebrate”, “invertebrate”, “zooplankton”, or other. If “other” is mentionned, the species will automatically be considered as producer and not as consumer. Capital and lowercase letters are allowed for the species category. Species category can also be provided in French.

Outputs : A data frame with the Niche attributes of each species countaining:

1. name = the species name
2. n = the log10(species body sizes in μm)
3. low = the lower bound of the species diet range (QR at 5%)
4. high= the higher bound of the species diet range (QR at 95%)
5. c = the center of the species diet range

```
get_niche_attributes<-function(name,body_size, species_category) {

  Niche<-data.frame(name=NA,n=NA,c=NA,low=NA,high=NA)

  for(i in 1:length(body_size)){

    Niche2<-data.frame(name=NA,n=NA,c=NA,low=NA,high=NA)

    # For primary producers
    if(!str_detect(species_category[i], regex("vertebrate", ignore_case = TRUE)) |
       !str_detect(species_category[i], regex("invertebrate", ignore_case = TRUE)) |
       !str_detect(species_category[i], regex("vertebre", ignore_case = TRUE)) |
       !str_detect(species_category[i], regex("invertebre", ignore_case = TRUE))|
       !str_detect(species_category[i], regex("zoop", ignore_case = TRUE))){
```

```
      Niche2$name=name[i]
      Niche2$n = body_size[i]
      Niche2$low = 0
      Niche2$high = 0
      Niche2$c = 0
    }

    # For vertebrates
    if(str_detect(species_category[i], regex("vertebrate", ignore_case = TRUE))&
       !str_detect(species_category[i], regex("inv", ignore_case = TRUE))|
       str_detect(species_category[i], regex("vertebre", ignore_case = TRUE))&
       !str_detect(species_category[i], regex("inv", ignore_case = TRUE))){
      qrsup = Param_regvert[[2]]
      qrinf = Param_regvert[[3]]
      Niche2$name=name[i]
      Niche2$n = body_size[i]
      Niche2$low = qrinf[1] + qrinf[2]*body_size[i]
      Niche2$high = qrsup[1] + qrsup[2]*body_size[i]
      Niche2$c = Niche2$low+(Niche2$high-Niche2$low)/2
    }

    # For invertebrates
    if(str_detect(species_category[i], regex("invertebrate", ignore_case = TRUE))|
       str_detect(species_category[i], regex("invertebre", ignore_case = TRUE))|
       str_detect(species_category[i], regex("zoop", ignore_case = TRUE))){
      qrsup = Param_reginvert[[2]]
      qrinf = Param_reginvert[[3]]
      Niche2$name=name[i]
      Niche2$n = body_size[i]
      Niche2$low = qrinf[1] + qrinf[2]*body_size[i]
      Niche2$high = qrsup[1] + qrsup[2]*body_size[i]
      Niche2$c = Niche2$low+(Niche2$high-Niche2$low)/2

    }
    Niche<-rbind(Niche,Niche2)
  }

  return(na.omit(Niche))
}
```

Function 2: L_fn2

Transform the parameters from get_niche_attributes into an binary interaction matrix from Gravel et al. 2013

Inputs:

1. name = the species name
2. n = the log10(species body sizes in μm)
3. low = the lower bound of the species diet range (QR at 5%)
4. high= the higher bound of the species diet range (QR at 95%)
5. c = the center of the species diet range
6. table= “NO” to only obtain the binary matrix, “YES” to only obtain the binary matrix + a data.frame with one observation = one interaction

Outputs :

A binary interaction matrix with 0 indicating absence of a link and 1 indicating the presence of a link with consumers in columns (j) and resources in rows (i) OR A list with the binary interaction matrix + a table referencing each link with :

1. Res = the resource name
2. Cons = the consumer name
3. Log10Size_Res = log10(resource body size)
4. Log10Size_Cons = log10(consumer body size)

```r
L_fn2 <- function(name,n,c,low,high,table) {

  S <- length(n)
  L <- matrix(0,nr=S,nc=S)

  for(j in 1:S)
    for(i in 1:S)
      if(n[i]>low[j] && n[i]<high[j]) L[i,j] = 1
  colnames(L) <-name
  rownames(L) <-name

  Table<-data.frame(Res=NA,Cons=NA,Log10Size_Res=NA,Log10Size_Cons=NA)
  for(i in 1:S){
    if(length(which(L[,j]==1))!=0){
      Table2 <- data.frame(Res=names(which(L[,j]==1)),
                           Cons=rep(colnames(L)[j],length(which(L[,j]==1))),
                           Log10Size_Res=n[which(L[,j]==1)],
                           Log10Size_Cons=n[j])}
    else{Table2<-data.frame(Res=NA,Cons=NA,Log10Size_Res=NA,Log10Size_Cons=NA)}
    Table <- rbind(Table,Table2)}

  if(table=="NO"){
    return(L)
  }
  if(table=="YES"){
    return(list(Bmat=L,Table=na.omit(Table)))
  }
}
```

Function3: Ref_L_Diet

Refine links for impossible results according to species diet trait. Fish do not eat primary producers. Carnivorous macroinvertebrates do not eat primary producers Other diet refinement can be implemented after applying the function as they are considered as site-specific.

Inputs:

1. Bmat = binary matrix of trophic links inferred from L_fn2 function with : colnames and rownames = names of species in the inventory
2. diet = "invP" or "inv" for invertebrates | "p"=piscivorous or "o"=omnivorous for fish | "prod" for primary producers
3. table = "YES" or "NO" to obtain or note the matrix with links refined
4. LinksTab = if Table is "YES" provide the table of links obtained with the function L_fn2

Outputs :

1. if table="NO", returns th Binary matrix after link refinement
2. if table="YES", returns th Binary matrix after link refinement + the table of links after links refinement

```r
Ref_L_Diet <- function(Bmat, diet,table,LinksTab) {
  if(table=="NO"){

    for(j in 1:ncol(Bmat)){
      for (i in 1:nrow(Bmat)){
        if(diet[j]=="omnivorous" & diet[i]=="prod" |

           diet[j]=="piscivorous" & diet[i]=="prod"){
          Bmat[i,j]<-0
        }else{Bmat[i,j]<-Bmat[i,j]}

        if(diet[j]=="invP" &
           diet[i]=="prod"){
          Bmat[i,j]<-0
        }else{Bmat[i,j]<-Bmat[i,j]}
      }
    }
    return(Bmat_ref=Bmat)
  }

  if (table == "YES") {
    for(j in 1:ncol(Bmat)){
      for (i in 1:nrow(Bmat)){
        if(length(which(Bmat[,j]==1))!=0){

          if(diet[j]=="omnivorous" & diet[i]=="prod" |
             diet[j]=="piscivorous" & diet[i]=="prod"){
            Bmat[i,j]<-0
          }else{Bmat[i,j]<-Bmat[i,j]}

          if(diet[j]=="invP" & diet[i]=="prod"){
            Bmat[i,j]<-0
          }else{Bmat[i,j]<-Bmat[i,j]}

        }else{Bmat[,j]<-0}
      }
    }

    for (j in 1:ncol(Bmat)) {
      for (i in 1:nrow(Bmat)) {
        if(Bmat[i,j]==0){
          LinksTab$Prey[LinksTab$Prey==rownames(Bmat)[i]&
                          LinksTab$Pred==colnames(Bmat)[j]]<-NA
        }else{

        }
      }
    }
    return(list(Bmat_ref = Bmat,Table_ref=na.omit(LinksTab)))
  }
}
```

Function 4: Ref_L_Hab

Refine links for impossible results according to the habitat trait

Inputs:

1. Bmat = binary matrix of trophic links inferred from L_fn2 function with : colnames and rownames = names of species in the inventory
2. habitat = “pel” or “ben” or “pel/ben”
3. Table = “YES” or “NO” to obtain or note the matrix with links refined

Outputs :

1. if Table=“NO”, returns th Binary matrix after link refinement
2. if Table=“YES”, returns th Binary matrix after link refinement and the table of links after links refinement

```r
Ref_L_Hab = function(Bmat, habitat, table,LinksTab) {
  if(table=="NO"){
    for(i in 1:ncol(Bmat)){
      for (j in 1:nrow(Bmat)){
        if(length(which(Bmat[,i]==1))!=0){
          if(habitat[i]=="pel" &
             habitat[j]=="ben" |
             habitat[i]=="ben" &
             habitat[j]!="pel"){
            Bmat[j,i]<-0
          }else{Bmat[j,i]<-Bmat[j,i]}
        }else{Bmat[,i]<-0}
      }
    }
    return(Bmat_ref=Bmat)
  }

  if (table == "YES") {
    for (i in 1:ncol(Bmat)) {
      for (j in 1:nrow(Bmat)) {
        if (length(which(Bmat[, i] == 1)) != 0) {
          if (habitat[i] == "pel" &
              habitat[j] == "ben" |
              habitat[i] == "ben" &
              habitat[j] == "pel") {
            Bmat[j, i] <- 0
          } else{
            Bmat[j, i] <- Bmat[j, i]
          }
        } else{
          Bmat[, i] <- 0
        }
      }
    }

    for (i in 1:ncol(Bmat)) {
      for (j in 1:nrow(Bmat)) {
        if(Bmat[j,i]==0){
          LinksTab$Prey[LinksTab$Prey==rownames(Bmat)[j]& LinksTab$Pred==colnames(Bmat)[i]]<-NA
        }else{
```

```
        }
      }
    }
    return(list(Bmat_ref = Bmat,Table_ref=na.omit(LinksTab)))
  }
}
```

Function 5: Weighting

Used to obtain the likelyhood of an occuring trophic link between a consumer and a ressource. This “weighting” is scaled to the resource body size range obtained from diet range for each consumer.

Inputs :

1. Niche_attributes = data frame resulting from the function “get_niche_attribute” with :

- names = species name also used as colnames/rownames for the binary matrix
- n = log10(species body size (μm))
- c = optimal center of the niche (log10(μm))
- low = lower bound of the niche range (log10(μm))
- high =higher bound of the niche range (log10(μm))

2. Bmat = initial binary interaction matrix

Outputs :

1. the “weighted”" interaction matrix

```
Weighting <- function(Niche_attributes,Bmat){
    for(j in 1:ncol(Bmat)){
    if(length(which(Bmat[,j]==1))!=0){
      Bmat[which(Bmat[,j]==1),j] <- dnorm(Niche_attributes$n[which(Bmat[,j]==1)],
                 mean=Niche_attributes$c[j],
                 sd=sd(seq(from=Niche_attributes$low[j],to=Niche_attributes$high[j],
                 by=((Niche_attributes$high[j]-Niche_attributes$low[j])/100))))/
                 max(dnorm(Niche_attributes$n[which(Bmat[,j]==1)],
                  mean=Niche_attributes$c[j],
                  sd=sd(seq(from=Niche_attributes$low[j],to=Niche_attributes$high[j],
                          by=((Niche_attributes$high[j]-Niche_attributes$low[j])/100)))))
    }else{Bmat[which(Bmat[,j]!=1),j]<-0}
  }
  return(Bmat)
}
```

Example: Inferrence and refinement of the trophic links among species in an inventory

Loading library and data

```
library(stringr)

#Parameters to calculate the consumers diet range (regressions quantiles)
load("Param_reginvert.Rdata") # For invertebrates
load("Param_regvert.Rdata")   # For vertebrates

#Loading of the species inventory created for the example
load("Example_SpInventory.Rdata")
DATA2<-DATA[order(DATA$bs,decreasing=TRUE),] # species are ordered by decreasing body size
DATA2$Log10bs<-log10(DATA2$bs) #Body size is transformed to log10
```

A) The resource body sizes range are reconstructed for consumers based on :

1. species category (i.e., primary producers, zooplankton,invertebrate, vertebrate)
2. body size

Note that rows corresponding to primary producers are automatically filled with 0.

```
bs_r<-get_niche_attributes(name=DATA2$Species,
                           body_size = DATA2$Log10bs,
                           species_category = DATA2$Category)
```

B) Inferrences of all trophic links (binary matrix)

```
Bmat<-L_fn2(name=bs_r$name,n=bs_r$n,c=bs_r$c,low=bs_r$low,high=bs_r$high,table="NO")
```

C) Links refinement based on consumers' diet

```
Bmat_Diet<-Ref_L_Diet(Bmat=Bmat, diet=DATA2$Diet,table="NO")
```

D) Links refinement based on consumers' habitat

```
Bmat_Hab<-Ref_L_Hab(Bmat=Bmat_Diet,habitat =DATA2$Habitat,table="NO")
# Note that supplementary refinement can be implemented depending on the ecosystems or the
# species studied.In this example fish and predatory invertebrates are not allowed to consume
# primary producers.
# Final binary matrix Mb is given by:
Mb<-Bmat_Hab
```

E) Weighting of refined trophic links

```
Mb_W<-Weighting(Niche_attributes = bs_r,Bmat=Mb)
```

F) Use weightings as resources i proportions in diet of consumer j

$$\omega_{ji} = \frac{WeightedLink_{ji}}{\sum_{i \in resources\ of\ j} WeightedLink_{ji}} \ (eq.1)$$

```
Wji<-Mb_W
Wji[,which(colSums(Wji)!=0)]<-t((1/colSums(Wji[,which(colSums(Wji)!=0)])) *
                                 t(Wji[,which(colSums(Wji)!=0)]))
```

G) Save matrices used in the simulations of population dynamics

```
save(DATA2,file="DATA2.Rdata")# Species inventory with supplementary data
save(Mb,file="Mb.Rdata") # Binary interaction matrix
save(Wji,file="Wji.Rdata") # Matrix of resources i proportions in diet of consumer j
```

Supplementary material of:
Combining food-web theory and population dynamics to assess the impact of invasive species

R-code part 2: Simulations of population dynamics

Chloé Vagnon, Rudolf P. Rohr

June 2021

Example: Simulations of population dynamics

Loading library and data

```
library("deSolve") # Package for calculations

load("DATA2.Rdata") # Species inventory created in the 1st part of the code example
load("Mb.Rdata")    # Binary interaction matrix
load("Wji.Rdata")   # Species proportions in consumer diet

# Load the parameters to convert body size to metabolic rate
load("bodymass.Rdata") # For conversion from body size to bodymass
load("metabolic.Rdata") # For conversion from body mass to metabolic rate
```

A) Parametrization of the dynamic model with constants from literature and allometric relationships

```
S <- length(DATA2$Species)       # Define the number of species (S)
Iprod <- which(colSums(Mb) == 0) # Define the primary producers (Iprod)
Cons <- which(colSums(Mb) > 0)   # Define the consumers (Cons)

# Log10(body size) is converted in Log10(body mass)
DATA2$Log10bm <- m_bodymass$coefficients[1] + m_bodymass$coefficients[2] * DATA2$Log10bs
# Log10(body mass) is converted in metabolic rate
DATA2$Log10mr <- m_metabolic$coefficients[1] +
  m_metabolic$coefficients[2]*DATA2$Log10bm + m_metabolic$coefficients[3]*DATA2$Log10bm^2

#Biotic capacity of primary producers
DATA2$K[Iprod] <- 10^(-0.77*DATA2$Log10bm[Iprod]-6)

# Maximum consumption rate
DATA2$y[DATA2$Category == 'Vertebrate'] <- 4
DATA2$y[DATA2$Category == 'Invertebrate' & DATA2$Diet=="invP"] <- 8
DATA2$y[DATA2$Category == 'Invertebrate' & DATA2$Diet=="inv"] <- 5
DATA2$y[DATA2$Category == 'Zooplankton'] <- 6.5
DATA2$y[DATA2$Diet == 'prod'] <- 1.69
```

```
# Allometric constant(Brose et al., 2006)
DATA2$ax[DATA2$Category %in% 'Vertebrate'] <- 0.88
DATA2$ax[DATA2$Category != 'Vertebrate'] <- 0.314

# Efficiency of predator consumption
DATA2$epsilon[DATA2$Carnivorous == 1] <- 0.85
DATA2$epsilon[DATA2$Carnivorous ==0] <- 0.45

# Handling time
h<-t(Mb)
for (j in 1:nrow(h)){
  #for invertebrates
 if(is.element(rownames(h)[j],
               DATA2$Species[DATA2$Category%in%c("Invertebrate","Zooplankton")])){
   h[j,which(h[j,]!=0)]<-1/DATA2$y[j]
   }
 else{
 h[j,which(h[j,]!=0)]<-(4.084*10^5)*(10^DATA2$Log10bm[is.element(DATA2$Species,
                                                                names(which(h[j,]!=0)))])*
   (10^(DATA2$Log10bm[j])^-0.75)
  }

}
```

B) Initialization of the simulations
The dynamic of primary producer i is given by:

$$\frac{dN_i}{dt} = r_i \cdot \left(1 - \frac{N_i}{K_i}\right) \cdot N_i - \sum_{j \in consumers\ of\ i} F_{ji}(\overrightarrow{N}) \cdot N_j \quad (eq.2)$$

Where the functional response (*i.e.*, the per capita consumption rate of consumer j on resource i) is given by:

$$F_{ji}(\overrightarrow{N}) = \frac{x_j \cdot y_j \cdot \omega_{ji} \cdot N_i}{1 + \sum_{k \in resources\ of\ j} h_{jk} \cdot x_j \cdot y_j \cdot \omega_{jk} \cdot N_k} \quad (eq.3)$$

The dynamic of consumer j is given by:

$$\frac{dN_j}{dt} = -m_i \cdot \left(\frac{N_j}{K_i}\right) \cdot N_i + \varepsilon_j \sum_{i \in resources\ of\ j} F_{ji}(\overrightarrow{N}) \cdot N_j - \sum_{j \in consumers\ of\ i} F_{lj}(\overrightarrow{N}) \cdot N_l \quad (eq.4)$$

```
# Model used to calculate abundances at each time step
dN <- function(t,N,p){
  Fij <- p$alpha / as.vector(1 + (p$h *p$alpha)  %*%  N)
  out <- N * (p$r - p$alpha_intra * N  +  p$epsilon * Fij %*% N - t(Fij) %*% N)
  return(list(out))
}
# Note that alpha is the product of the metabolic rate mass dependant (xj), the maximum
# consumption rate (yj) and the matrix of resource proportions indiet of consumers (wij).
# It represents an interaction force, allometrically parameterized in our study but that
# can be parameterized with other technics.
```

C) Calulation of the abundances along time

```
N_rand <- 10               # Number of simulations
time_step <- seq(0,19999,1) # Time steps
Alive_sp <- rep(NA,N_rand)  # Vector allocation for alive species
Output<- array(NA,c(N_rand,length(time_step),S)) # Large array for stocking outputs


for (i in 1:N_rand){
  assign("last.warning", NULL, envir = baseenv())

  #Metabolic rate and noise simulated with the rnorm
  xj<- 10^(DATA2$Log10mr-DATA2$Log10bm)+ rnorm(S, mean=0, sd=0.001*(10^DATA2$Log10mr))


  # Growth
  r <- xj
  r[Cons] <- -r[Cons] * DATA2$ax[Cons]


  # alpha
  alpha <- (xj * DATA2$y) * t(Wji)
  alpha_intra <- rep(0,nrow(alpha))
  alpha_intra[Iprod] <- r[Iprod]/DATA2$K[Iprod] #intraspecific regulation for Iprod

  #List of parameters to induce in the equa diff computing
  p <- list(alpha = alpha, alpha_intra = alpha_intra, r = r, epsilon = DATA2$epsilon, h=h)

  # Initialization of initial  abundances
  N0 <- sort(round(runif(S, min=0.15, max=1), digits=5), decreasing = F)

  # Calculatin of results from differential equations
  out <- ode(y = N0, times = time_step, func = dN, parms = p)

  if (length(warnings())==0){    #Avoid warning messages
    N_equ <- out[dim(out)[1],-1] # N at the equilibrium
    alive <- N_equ > 1e-6 # Computing of species still alive

    Alive_sp[i] <- sum(alive)
    Output[i,,] <- as.matrix(out[,-1])
  }
}
```

Supporting information

Combining food web theory and population dynamics to assess the impact of invasive species

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This document is divided into 6 parts:

1. List of species clusters used in this study
2. Selection of *Silurus glanis* body sizes
3. Parametrization of the dynamic model and sensitivity analysis.
4. Complementary results for RAD analyses (Relative Abundance Differences).
5. Details of classified ecological interactions
6. Interaction strengths in the food-web.

Part 1. List of species clusters used in this study

Table S1. Species clusters characteristics

Superkingdom (Eukaryota)	Category	Phylum / subphylum	Class	Order	Family	Average body size (µm)	Lake Compartment
Pluricellular	Vertebrate	Vertebra	Actinopterygii	Esociformes	*Esocidae*	900000	Pelagic/Littoral
Pluricellular	Vertebrate	Vertebra	Actinopterygii	Salmoniformes	*Salmonidae*	400000	Pelagic/Littoral
Pluricellular	Vertebrate	Vertebra	Actinopterygii	Gadiformes	*Lotidae*	325000	Littoral
Pluricellular	Vertebrate	Vertebra	Actinopterygii	Cypriniformes	*Cyprinidae*	268333	Pelagic/Littoral
Pluricellular	Vertebrate	Vertebra	Actinopterygii	Siluriformes	*Ictaluridae*	225000	Littoral
Pluricellular	Vertebrate	Vertebra	Actinopterygii	Perciformes	*Percidae*	200000	Pelagic/Littoral
Pluricellular	Vertebrate	Vertebra	Actinopterygii	Scorpaeniformes	*Cottidae*	90000	Littoral
Pluricellular	Invertebrate	Crustacea	Malocostraca	Decapoda	*Astacidae*	87500	Littoral
Pluricellular	Vertebrate	Vertebra	Actinopterygii	Blennioidei	*Blenniidae*	80000	Littoral
Pluricellular	Vertebrate	Vertebra	Actinopterygii	Perciformes	*Centrarchidae*	70000	Littoral
Pluricellular	Invertebrate	Crustacea	Malocostraca	Decapoda	*Cambaridae*	62500	Littoral
Pluricellular	Invertebrate	Mollusca	Bivalvia	Myoida	*Dreissenidae*	25000	Littoral
Pluricellular	Invertebrate	Hexapoda	Insecta	Odonata	*Coenagrionidae*	20500	Littoral
Pluricellular	Invertebrate	Annelida	Clitellata	Rhynchobdellida	*Glossiphoniidae*	19000	Littoral
Pluricellular	Invertebrate	Hexapoda	Insecta	Odonata	*Gomphidae*	18500	Littoral
Pluricellular	Invertebrate	Hexapoda	Insecta	Odonata	*Libellulidae*	18500	Littoral
Pluricellular	Invertebrate	Hexapoda	Insecta	Ephemera	*Ephemeridae*	16250	Pelagic/Littoral
Pluricellular	Invertebrate	Crustacea	Malocostraca	Amphipoda	*Gammaridae*	15250	Littoral

Table S1 continued.

Superkingdom (Eukaryota)	Category	Phylum / subphylum	Class	Order	Family	Average body size (µm)	Lake Compartment
Pluricellular	Invertebrate	Arthropoda	Insecta	Lepidoptera	*Crambidae*	13500	Littoral
Pluricellular	Zooplankton	Crustacea	Branchiopoda	Cladocera	*Cercopagididae*	12500	Pelagic
Pluricellular	Zooplankton	Crustacea	Branchiopoda	Cladocera	*Leptodoridae*	12500	Pelagic
Pluricellular	Invertebrate	Arthropoda	Insecta	Trichoptera	*Polycentropodidae*	12175	Pelagic/Littoral
Pluricellular	Invertebrate	Mollusca	Gastropoda	Basommatophora	*Physidae*	9175	Littoral
Pluricellular	Invertebrate	Hexapoda	Insecta	Trichoptera	*Leptoceridae*	8650	Pelagic/Littoral
Pluricellular	Invertebrate	Hexapoda	Insecta	Diptera	*Chaoboridae*	8500	Pelagic/Littoral
Pluricellular	Invertebrate	Hexapoda	Insecta	Diptera	*Empididae*	8000	Pelagic/Littoral
Pluricellular	Invertebrate	Hexapoda	Insecta	Trichoptera	*Ecnomidae*	7700	Pelagic/Littoral
Pluricellular	Invertebrate	Mollusca	Bivalvia	Verenoida	*Sphaeriidae*	7682	Littoral
Pluricellular	Invertebrate	Hexapoda	Insecta	Diptera	*Chironomidae*	7171	Pelagic/Littoral
Pluricellular	Invertebrate	Hexapoda	Insecta	Ephemeroptera	*Baetidae*	6500	Pelagic/Littoral
Pluricellular	Invertebrate	Hexapoda	Insecta	Trichoptera	*Beraeidae*	6400	Pelagic/Littoral
Pluricellular	Invertebrate	Hexapoda	Insecta	Trichoptera	*Psychomiidae*	6400	Pelagic/Littoral
Pluricellular	Invertebrate	Mollusca	Gastropoda	Basommatophora	*Lymnaeidae*	6000	Littoral
Pluricellular	Invertebrate	Mollusca	Gastropoda	Basommatophora	*Planorbidae*	5500	Littoral
Pluricellular	Invertebrate	Mollusca	Gastropoda	Heterostropha	*Valvatidae*	5500	Littoral
Pluricellular	Invertebrate	Mollusca	Gastropoda	Littorinimorpha	*Bithyniidae*	5000	Littoral
Pluricellular	Invertebrate	Hexapoda	Insecta	Ephemeroptera	*Caenidae*	4500	Pelagic/Littoral
Pluricellular	Invertebrate	Hexapoda	Insecta	Trichoptera	*Hydroptilidae*	3850	Pelagic/Littoral

Table S1 continued.

Superkingdom (Eukaryota)	Category	Phylum / subphylum	Class	Order	Family	Average body size (µm)	Lake Compartment
Pluricellular	Invertebrate	Mollusca	Gastropoda	Littorinimorpha	*Tateidae*	3750	Littoral
Pluricellular	Invertebrate	Hexapoda	Insecta	Diptera	*Ceratopogonidae*	1900	Littoral
Pluricellular	Zooplankton	Crustacea	Branchiopoda	Diplostraca	*Daphniidae*	1820	Pelagic
Pluricellular	Invertebrate	Hexapoda	Insecta	Heteroptera	*Corixidae*	1625	Littoral
Pluricellular	Zooplankton	Crustacea	Maxillopoda	Cyclopoida	*Cyclopidae*	1050	Pelagic
Pluricellular	Zooplankton	Crustacea	Branchiopoda	Cladocera	*Sididae*	895	Pelagic
Pluricellular	Zooplankton	Rotifera	Eurotratoria	Ploima	*Asplanchnidae*	850	Pelagic
Pluricellular	Zooplankton	Rotifera	NA	Ploima	*Brachionidae*	725	Pelagic
Pluricellular	Zooplankton	Crustacea	Branchiopoda	Cladocera	*Bosminidae*	447	Pelagic
Pluricellular	Zooplankton	Rotifera	NA	NA	*Concochilidae*	225	Pelagic
Unicellular	Phytobenthos	Ochrophyta	Chrysophyceae	NA	NA	61	Littoral
Unicellular	Phytoplankton	Ochrophyta	Chrysophyceae	NA	NA	61	Pelagic
Unicellular	Phytoplankton	Ochrophyta	Diatoms	NA	NA	60	Pelagic
Unicellular	Phytoplankton	Myzozoa	Dinophyceae	NA	NA	50	Pelagic
Unicellular	Phytobenthos	Chlorophyta	Chlorophyceae	NA	NA	35	Littoral
Unicellular	Phytoplankton	Chlorophyta	Chlorophyceae	NA	NA	35	Pelagic
Unicellular	Phytobenthos	Cryptophyta	Cryptophyceae	NA	NA	30	Littoral
Unicellular	Phytoplankton	Cryptophyta	Cryptophyceae	NA	NA	30	Pelagic
Unicellular	Phytobenthos	Ochrophyta	Diatoms	NA	NA	29	Littoral
Unicellular	Phytoplankton	NA	Zygophyceae	NA	NA	25	Pelagic

Part 2: Selection of *Silurus glanis* body sizes.

The directed connectance (C) was selected to study the changes in food web topologies and was calculated as follows:

$$C = \frac{l}{S^2}$$

with l the number of links and S the number of species clusters in the food-web. Complementarily, the trophic vulnerability of species cluster (*TV* sum of links with their predators) the trophic generality (*TG* sum of links with their prey) and degree (*D,* sum of *TV* and *TG*) were also compared for the three *S. glanis* sizes retained.

The absolute changes of *C* following the invasion of *S. glanis* of different body sizes were limited due to the weak proportional change of number of species (+ 1.2%) and links (+ 2.4% of links on average) within the food-webs (Figure S1a). Yet, clear variations of directed connectance could be identified for three body sizes: 40 cm, 85 cm and 150 cm. Most variations occurred for *S. glanis* body sizes up to 85 cm and were characterized by a decrease of C while it remains steady for larger *S. glanis*. Consequently, we selected *S. glanis* of 40 cm, 85 cm and 150 cm to simulate scenarios that corresponded to the most noticeable changes in the foodweb topology while their degree ($D_{S40} = 14$, $D_{S85} = 7$, $D_{S150} = 10$) and their trophic position ($TP_{S40} = 3.9$, $TP_{S85} = 4.2$, $TP_{S150} = 4.5$) also differed sufficiently to suggest possible variations in their impacts on the general peri-alpine lake foodweb.

The 3D representations of the non-invaded food-web and of the invaded food-web highlighted the general structure of the food-webs and the high trophic position of each *S. glanis* compared to other species clusters. (Fig. S1b and c). This apex position was confirmed by the absence of predators for the three body sizes of *S. glanis* and thus did not influence the trophic generality of consumers but increased the trophic vulnerability of invertebrates and fish (Figure S2.).

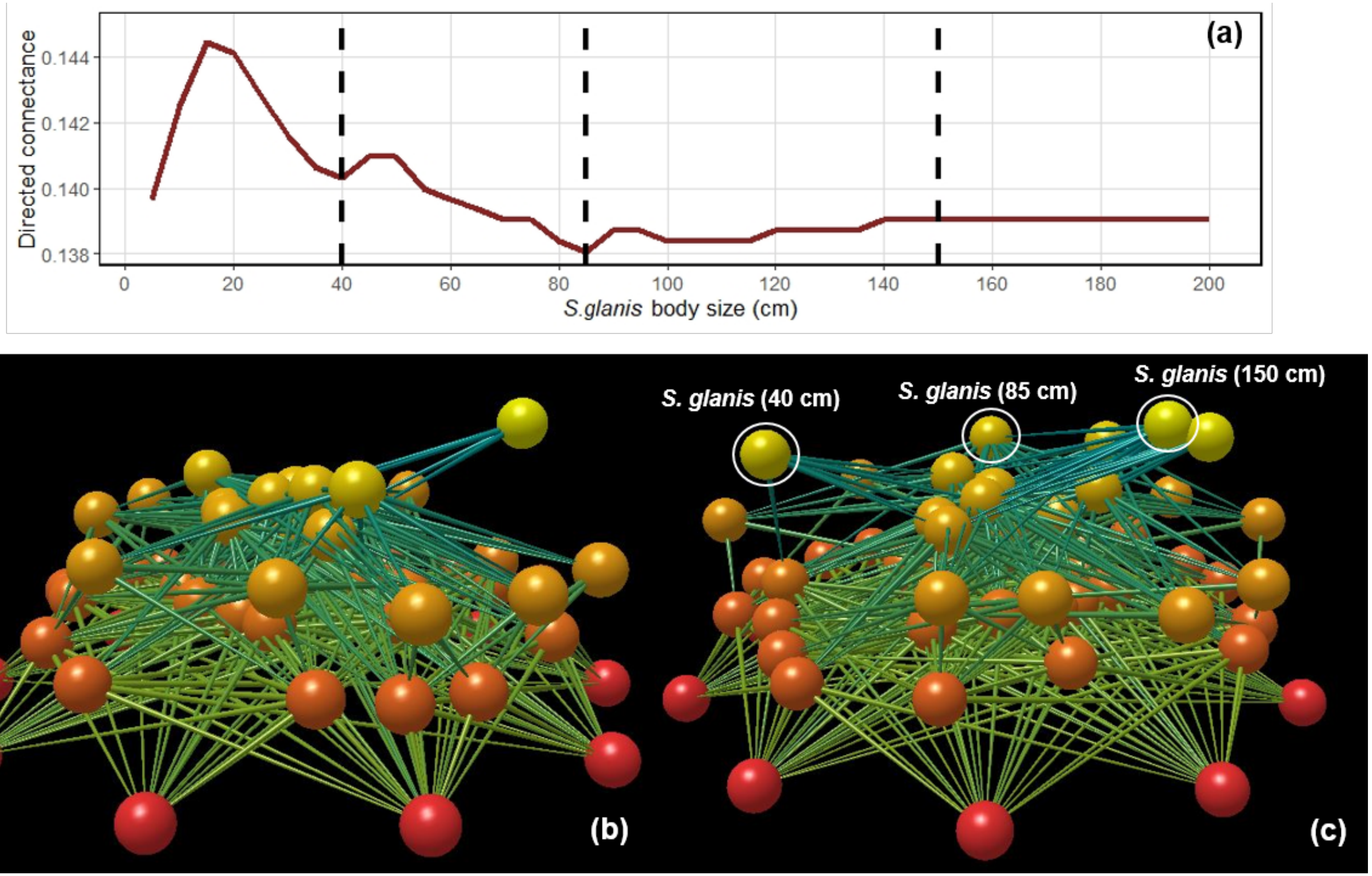

Figure S1: Body size selection (corresponding to dashed lines) based on clear-cut breaks of directed connectance of the global peri-Alpine lake food-web along *S. glanis* body sizes (a) and 3D representations of the food-web without *S. glanis* (b) and of the invaded food-web (c). Images representing 3D food-webs were produced with Network3D (Yoon et al., 2004).

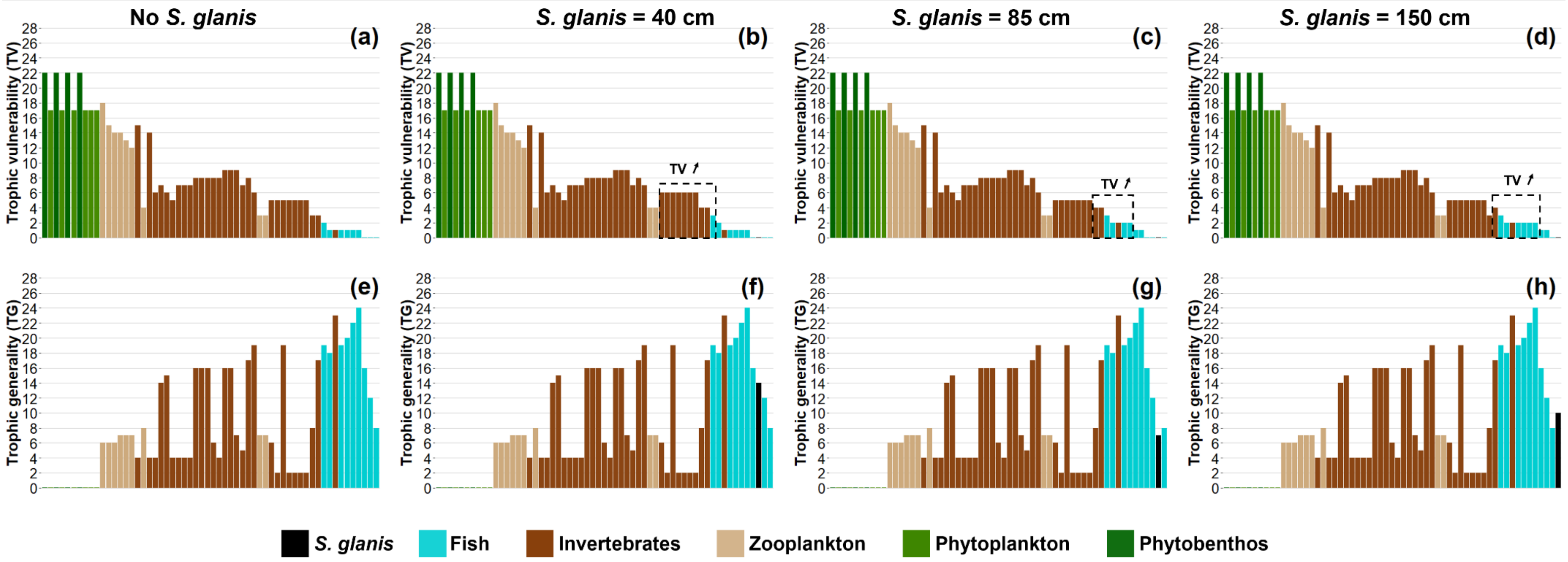

Figure S2: Species metrics in the food-web without *S. glanis* (1st column), with *S. glanis* of 40 cm (2nd column), 85 cm (3rd column) and 150 cm (4th column). Species clusters in barplots are organized by increasing body size from left to right. Dashed squares represent species clusters for which trophic vulnerability increased in presence of *S. glanis*.

Part 3. Parametrization of the dynamic model and sensitivity analysis.

Table S2: Values of the different parameters used to process the dynamic simulations.

Parameters	Definition	Values	References
y	Maximum consumption rate	$y_{Vertebrate} = 4$ $y_{CarnivorousInvertebrate} = 8$ $y_{NoCarnivorousInvertebrate} = 5$ $y_{Zooplankton} = 6.5$ $y_{Unicellular} = 1.69$	Brown, 2004 Brown, 2004 Jacobsen, 1994 Hansson, 1996 Flynn & Raven, 2017
ax	Allometric constant	$ax_{EctothermVertebrate} = 0.88$ $ax_{Invertebrate} = 0.314$	Brose *et al*., 2006 Brose *et al*., 2006
ε	Efficiency of predator consumption	$\mathcal{E}_{Carnivorous} = 0.85$ $\mathcal{E}_{Herbivorous} = 0.45$	Brown, 2004 Brown, 2004
K	Biotic capacity of basal species	$K = 10^{(-0.77*log10(m[basal_{species}]-6)}$	Brown, 2004
h	Handling time	$h_{Vertebrates} = 4.084.\, 10^5\, m[prey]\, m\, [pred]^{-0.75}$ $h_{Invertebrates} = \frac{1}{y}$	Kalinkat *et al.,* 2013; Brose, 2010; Kiørboe, 2017; Koen-Alonzo, 2007
bm	Body mass (g)	$log_{10}(m) = 3.24 log_{10}(body\ size) - 15.465$	Data fitted for this study from Delong *et al.* 2010 and Makarieva *et al.* 2008
mr	Metabolic rate	$log_{10}(mr) = 0.71m - 0.08bm^2 - 3.125$	Data fitted for this study from Delong *et al.* 2010 and Makarieva *et al.* 2008
x	Metabolic rate mass dependant	$x = 10^{(log_{10}(mr) - log_{10}(bm))}$	Brose *et al*., 2006

Sensitivity − We assessed the model sensitivity by implementing different extent of metabolic noise on the species clusters metabolic rates x_j and explored its influence on *MRAD* (median value of relative abundance differences *RAD*) obtained for fish, invertebrates, phytoplankton, phytobenthos and zooplankton. To simulate metabolic noises, a normal distribution was used with a mean fixed at 0 and varying standard deviation set at 0.1 %, 0.5 %, 1 %, 5%, 10 % and 20 % of x_j. The parameter N_0 was still the same for the 200 simulations to avoid initial abundances bias.

Density distributions are shown for fish, invertebrates, zooplankton, phytobenthos and phytoplankton for metabolic rate at 0 % (Figure S3), 0.1 % (Figure S4), 0.5 % (Figure S5), 1 % (Figure S5), 5 % (Figure S7), 10 % (Figure S8) and 20 % (Figure S9).

MRAD above 200 (median value of relative abundances differences 4 times higher) were not accounted in Kernel density plots as they represented anecdotal fractions of simulations for the different metabolic noises (0.29 %, 0.46 %, 1.18 %, 2.21 %, 3.42 % and 5.93 % respectively; Fig. S10). *MRAD* above 200 found in simulations with low metabolic noises concerned only fish and progressively corresponded to phytoplankton and phytobenthos to finally concern fish, primary producers and invertebrates in simulations with the highest metabolic noise.

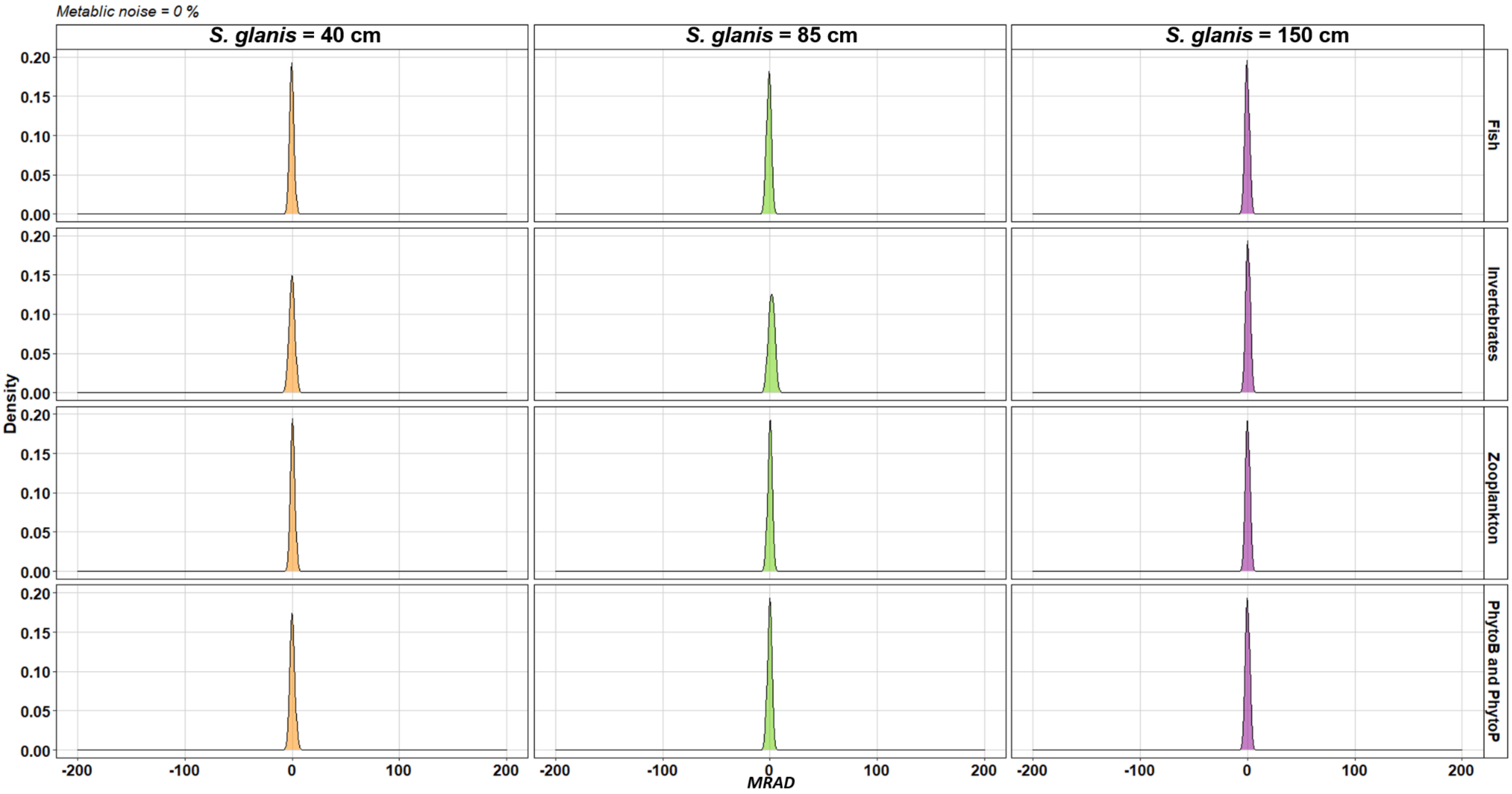

Figure S3: Density distribution of *MRAD* without considering metabolic noise in simulations.

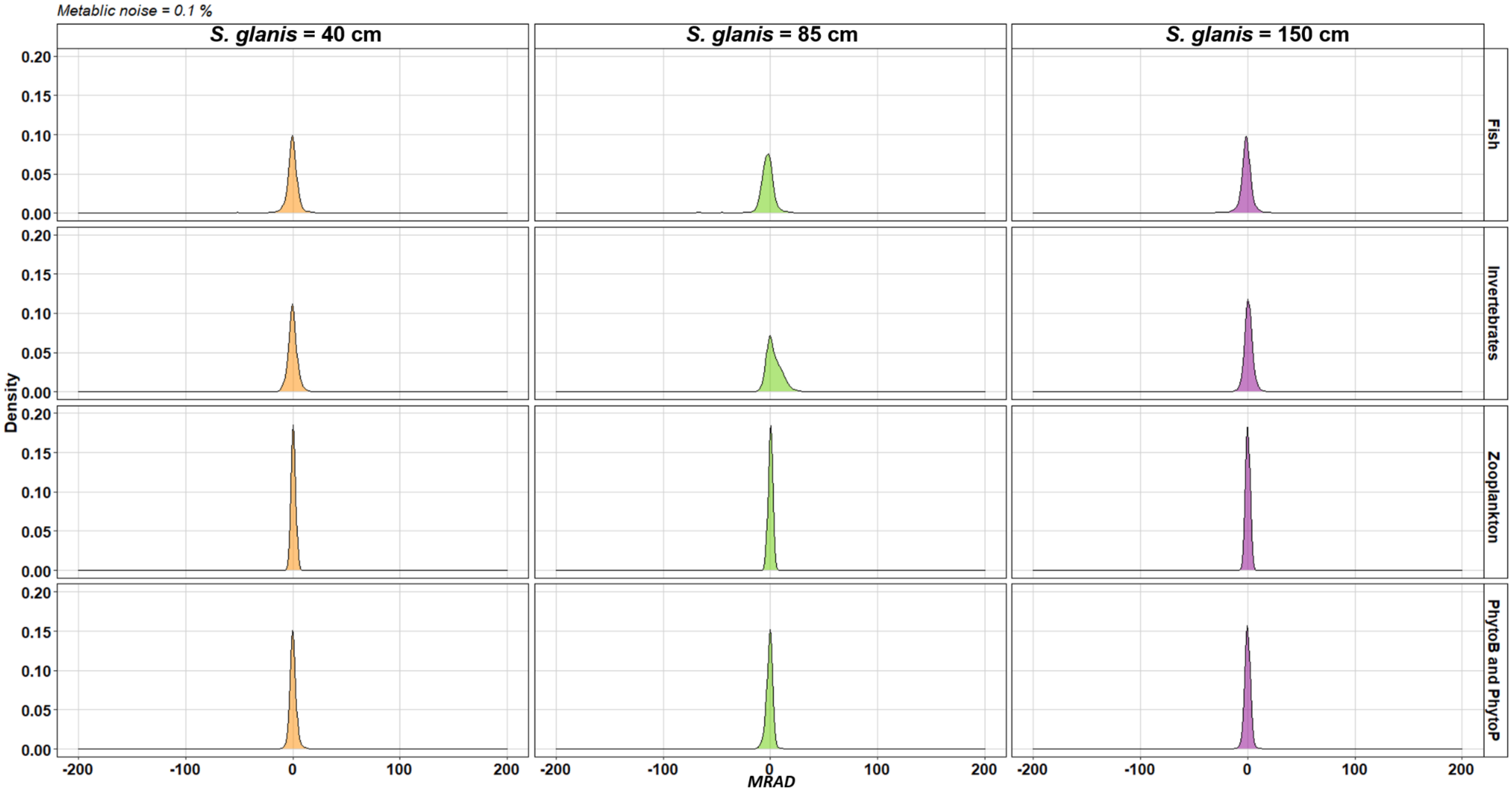

Figure S4: Density distribution of *MRAD* considering a metabolic noise of 0.1 % of M_i in simulations.

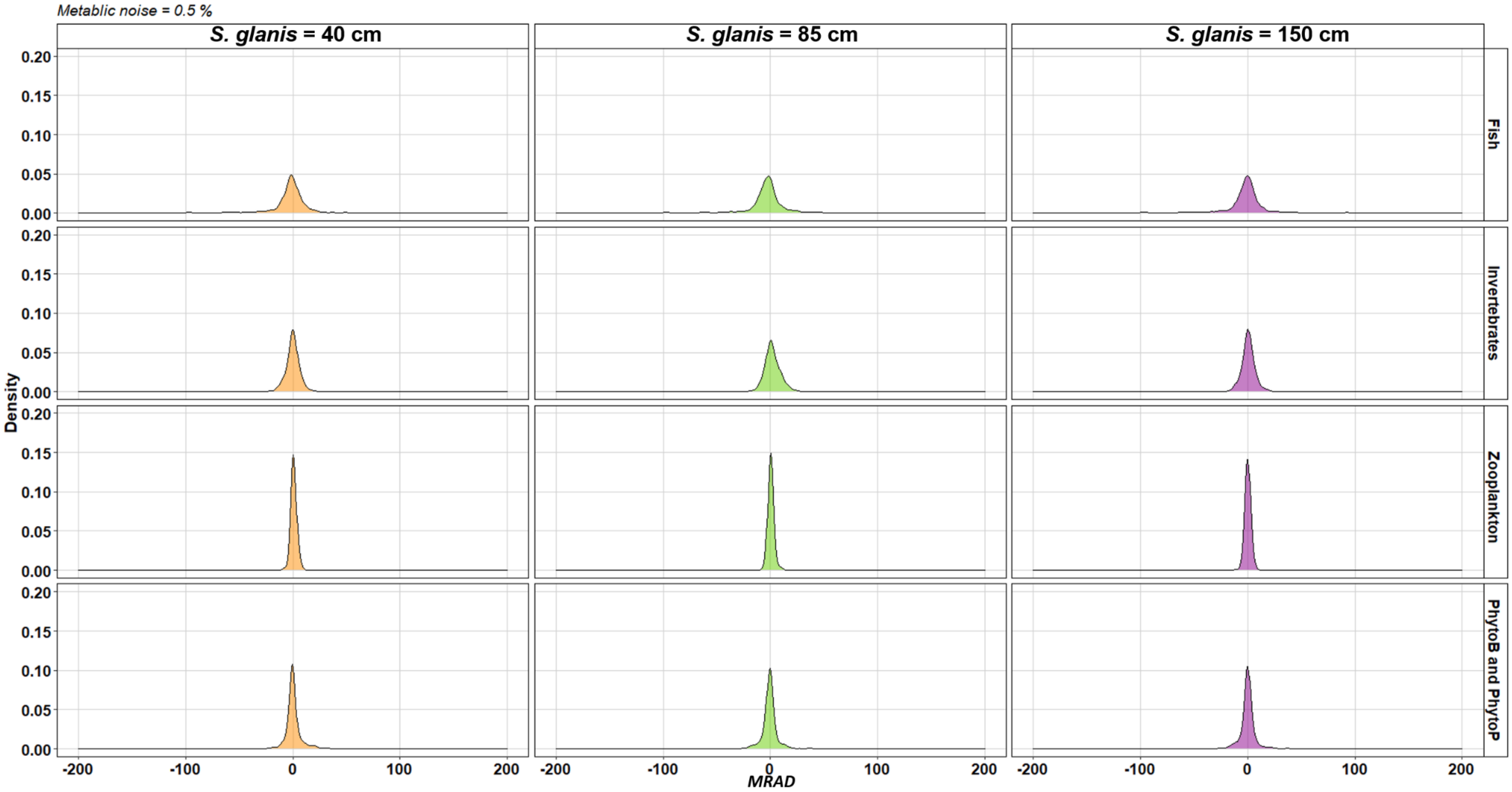

Figure S5: Density distribution of *MRAD* considering a metabolic noise of 0.5 % of M_i in simulations.

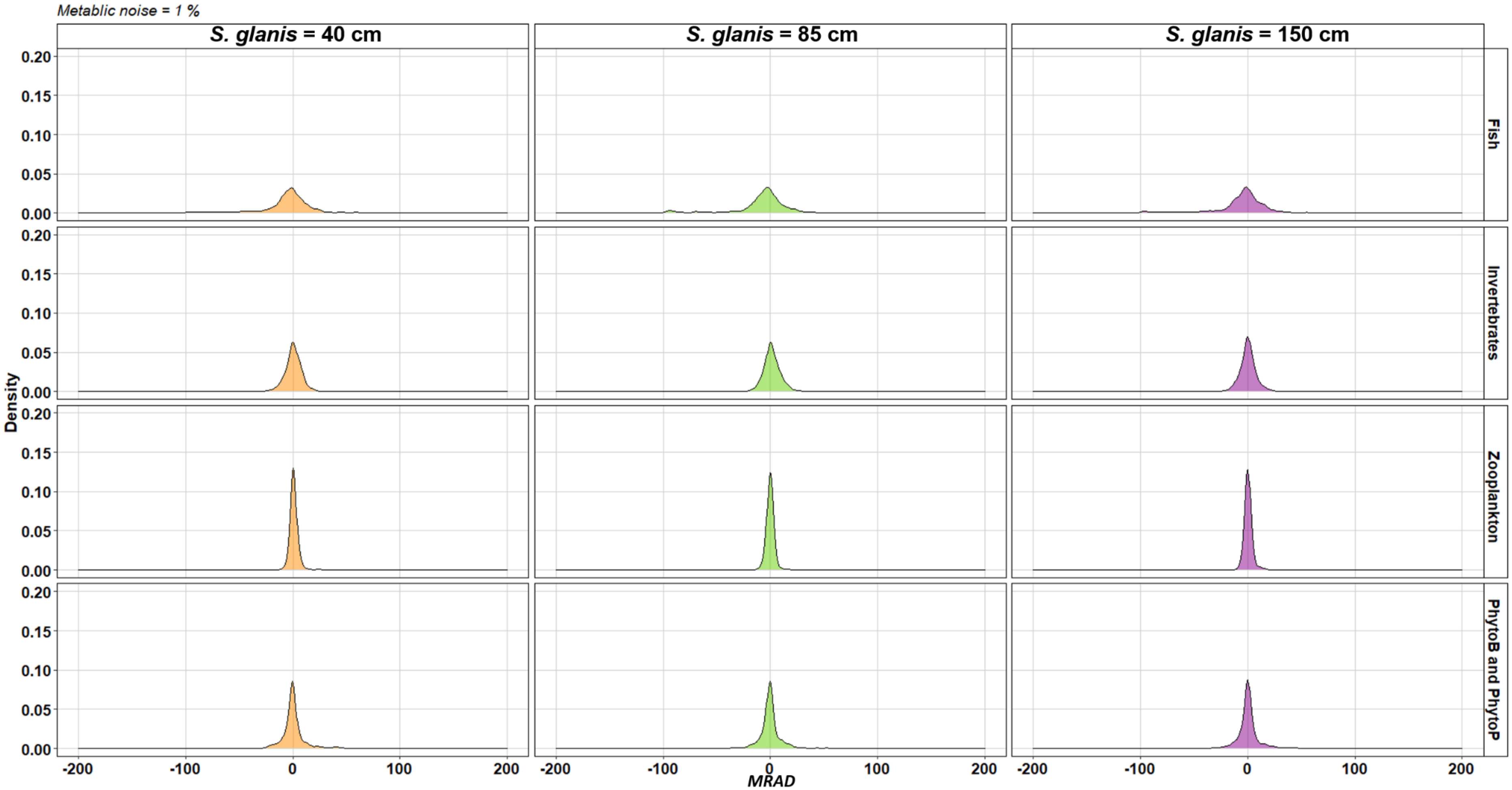

Figure S6: Density distribution of *MRAD* considering a metabolic noise of 1 % of M_i in simulations.

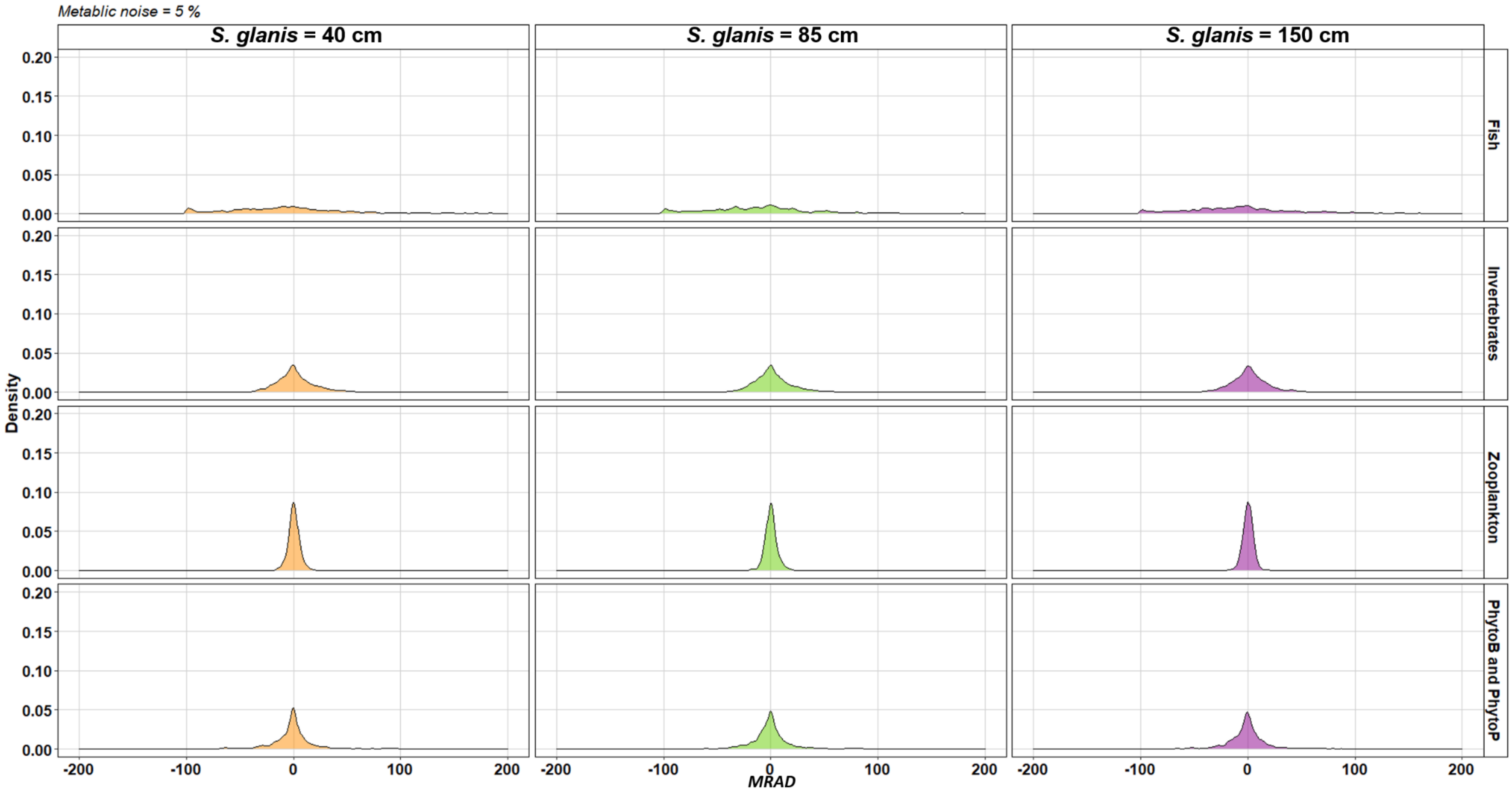

Figure S7: Density distribution of *MRAD* considering a metabolic noise of 5 % of M_i in simulations.

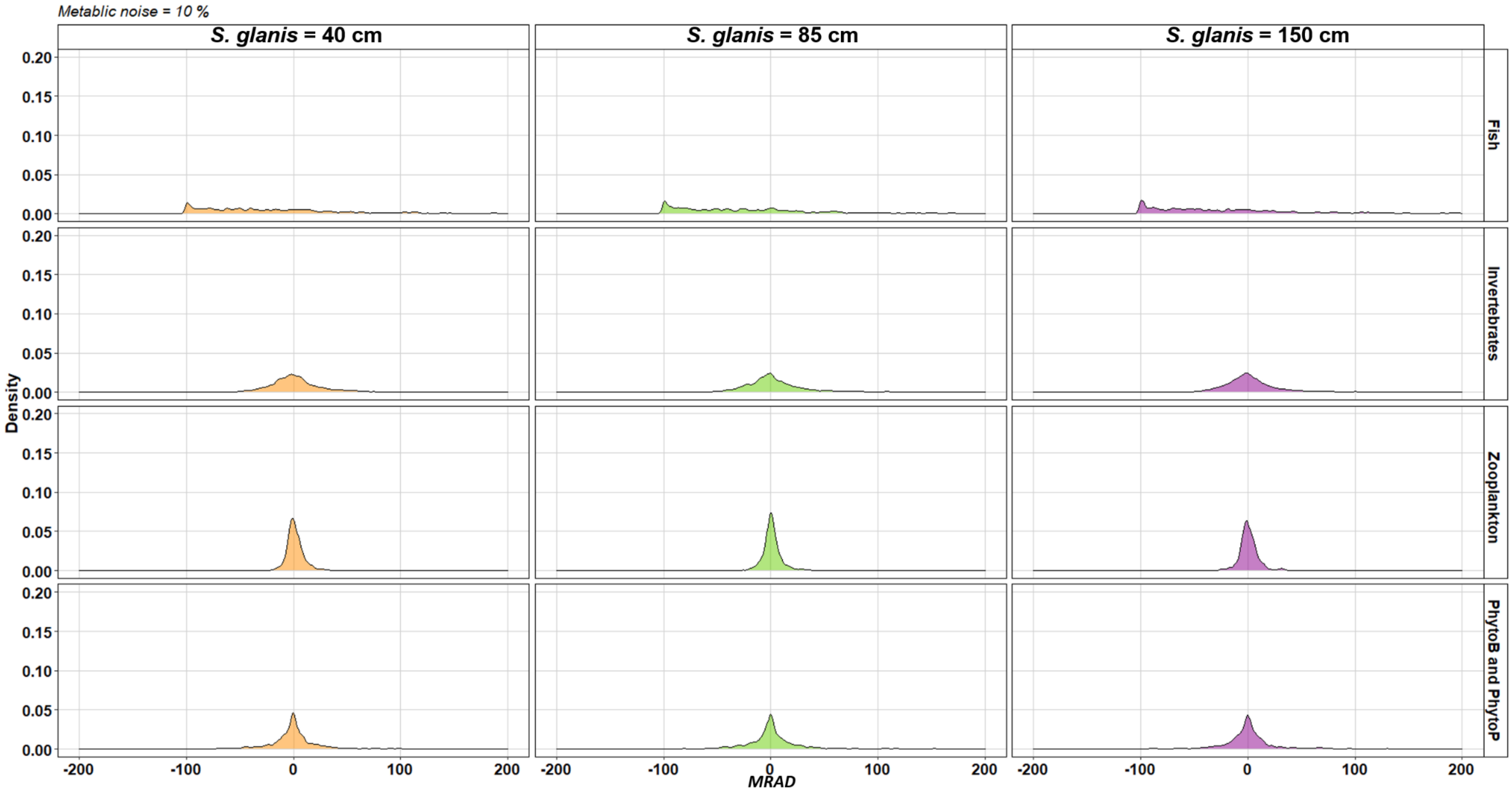

Figure S8: Density distribution of *MRAD* considering a metabolic noise of 10 % of M_i in simulations.

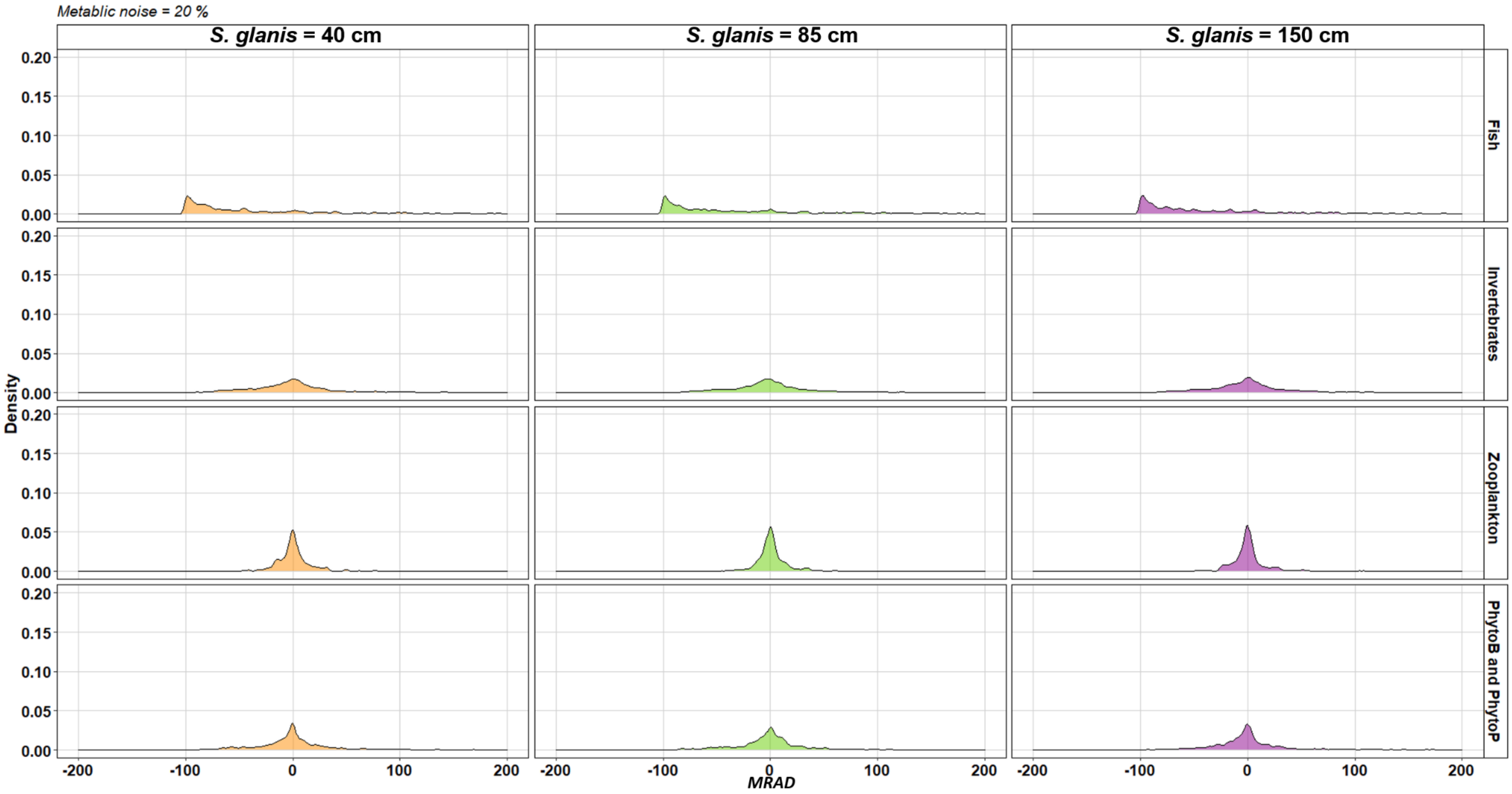

Figure S9: Density distribution of *MRAD* considering a metabolic noise of 20 % of M_i in simulations.

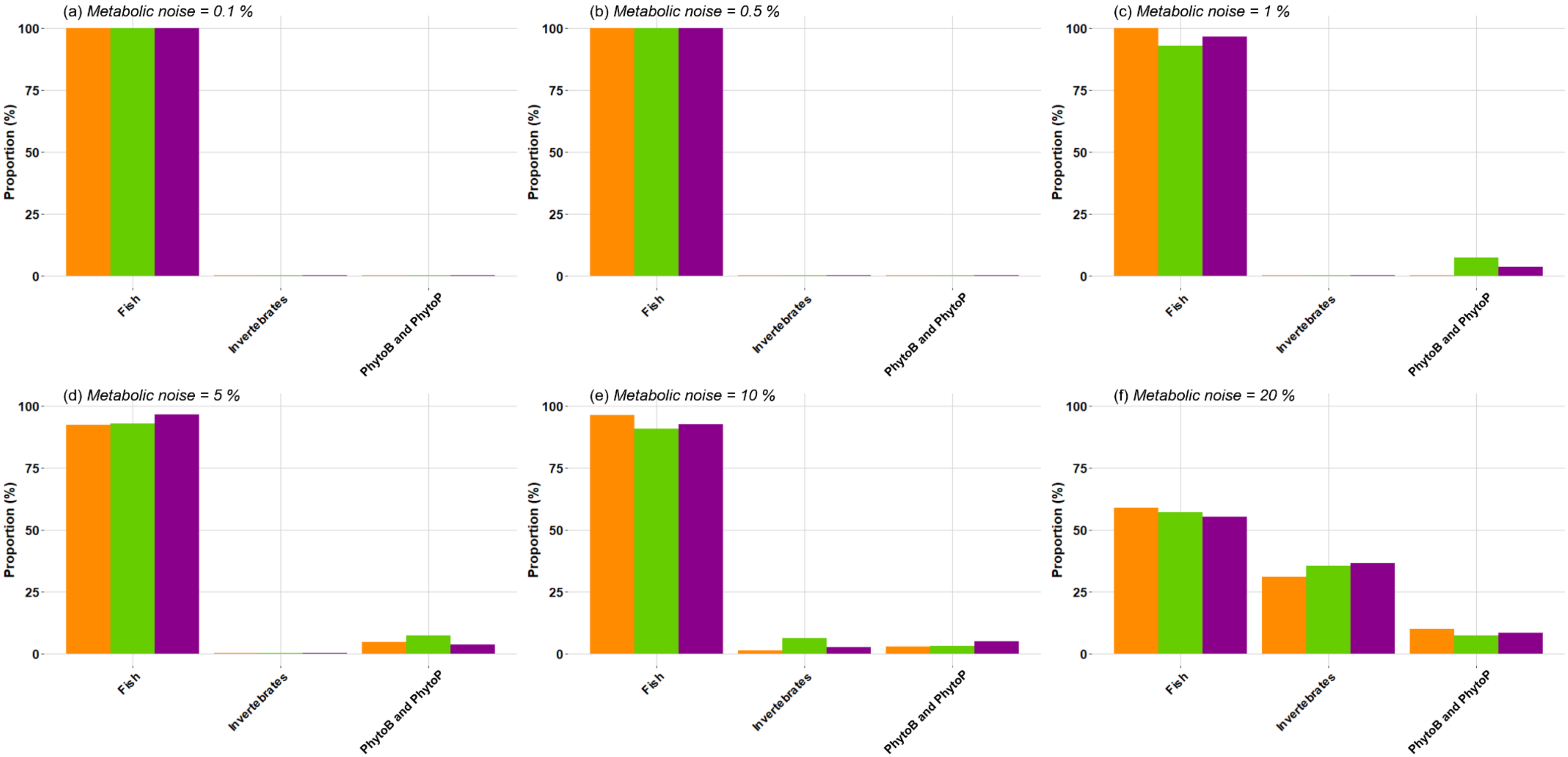

Figure S10: Repartition of *MRAD* above 200 among fish, invertebrates, phytobenthos (PhytoB) and phytoplankton (PhytoP) for each metabolic noise considering the 200 simulations.

Part 4: Complementary results for *RAD* analyses (Relative Abundance Differences).

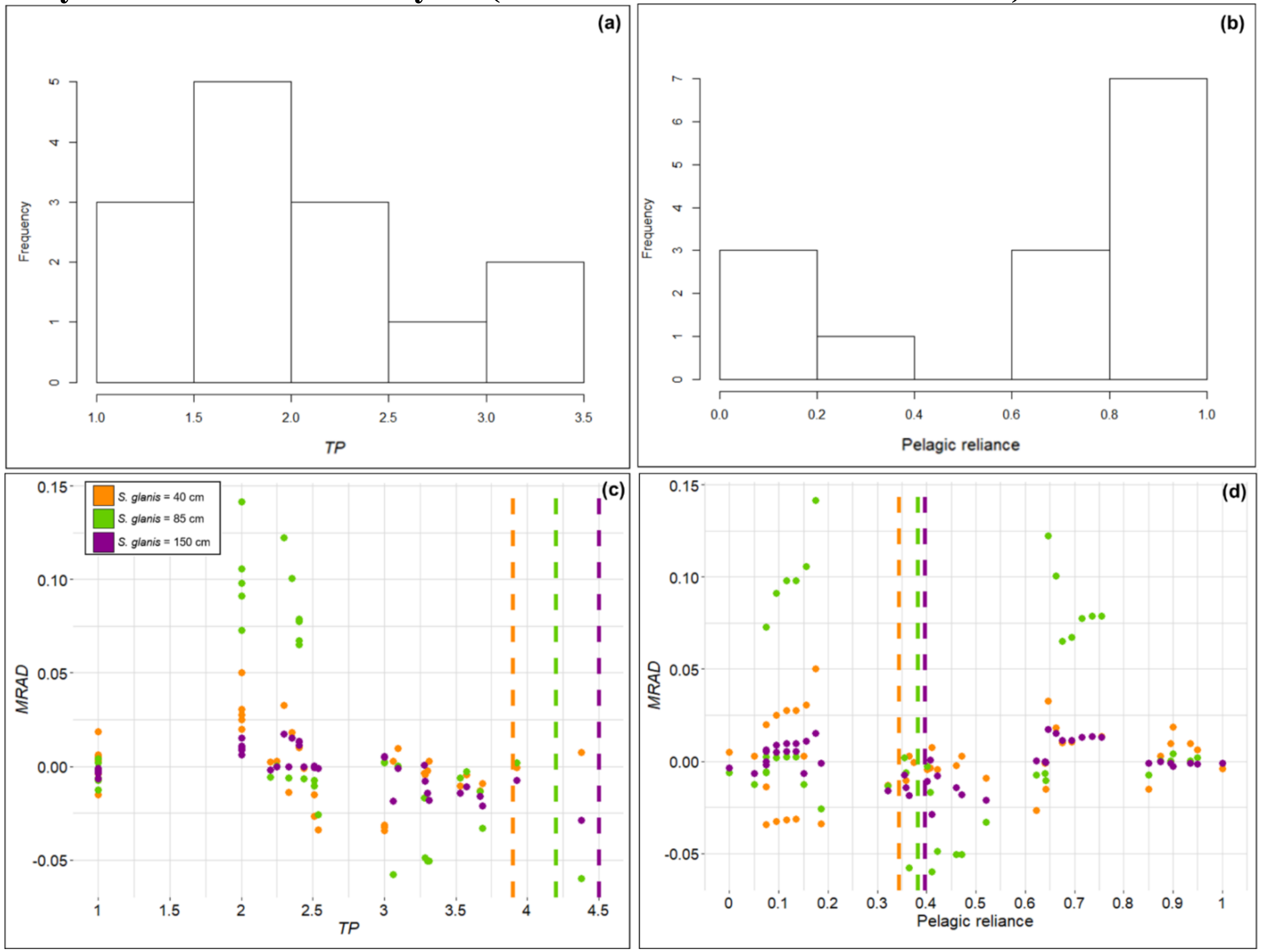

Figure S11: Effect of *S. glanis* (*MRAD*) on species clusters regarding their trophic position and their pelagic reliance. (a) corresponds to a histogram of extinct species clusters according to their *TP* and (b) is a histogram of extinct species clusters according to their pelagic reliance. (c) and (d) correspond to effects of *S. glanis* according to the *TP* and to the pelagic reliance of non-extinct species clusters. In (c) and (d) dashed lines are *TP* and pelagic reliance of the three *S. glanis*, respectively.

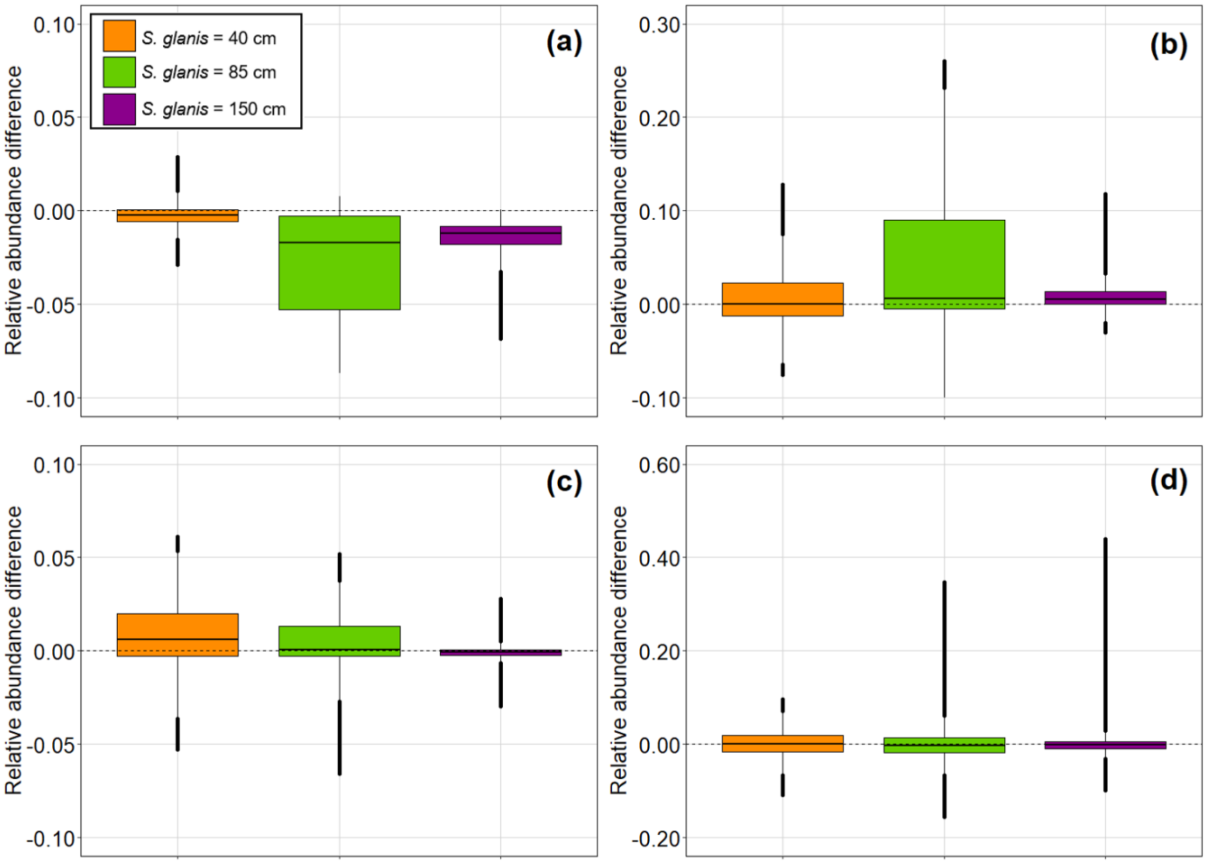

Figure S12: Relative abundance differences (*RAD*) along the 20 000 time steps in presence of each *S. glanis* body size after taxonomic aggregation of species clusters. Results are presented for all fish (a), invertebrates (b), zooplankton (c), phytoplankton and phytobenthos species clusters (d).

Part 5. Details of classified ecological interactions

Table S3: Trophic positions of species clusters and interaction involved in each scenario depending on extinct and non-extinct species clusters. The sign "–" corresponds to an interaction with negative impact (*MRAD* < 0). Contrary, the sign "+" is used when the interaction seems favourable to the species cluster. The dashed line in the table correspond to the separation between extinct and non-extinct species clusters.

Species cluster	**Category**	**Trophic Position**	**State**	***S. glanis* = 40 cm**	***S. glanis* = 85 cm**	***S. glanis* = 150 cm**
Concochilidae	Invertebrate	2.0	Extinct	Trophic cascade -	Trophic cascade -	Trophic cascade -
Corixidae	Invertebrate	2.0	Extinct	Trophic cascade -	Trophic cascade -	Trophic cascade -
Bosminidae	Zooplankton	2.0	Extinct	Trophic cascade -	Trophic cascade -	Trophic cascade -
Ceratopogonidae	Invertebrate	2.0	Extinct	Trophic cascade -	Trophic cascade -	Trophic cascade -
Brachionidae	Zooplankton	2.0	Extinct	Trophic cascade -	Trophic cascade -	Trophic cascade -
Cryptophyceae_ben	Phytobenthos	1.0	Extinct	Trophic cascade -	Trophic cascade -	Trophic cascade -
Asplanchnidae	Zooplankton	2.1	Extinct	Trophic cascade -	Trophic cascade -	Trophic cascade -
Sididae	Zooplankton	2.1	Extinct	Trophic cascade -	Trophic cascade -	Trophic cascade -
Cyclopidae	Zooplankton	2.1	Extinct	Trophic cascade -	Trophic cascade -	Trophic cascade -
Chironomidae	Invertebrate	3.0	Extinct	Trophic cascade -	Trophic cascade -	Trophic cascade -
Zygophyceae	Phytoplankton	1.0	Extinct	Trophic cascade -	Trophic cascade -	Trophic cascade -
Chaoboridae	Invertebrate	3.0	Extinct	Trophic cascade -	Trophic cascade -	Trophic cascade -
Cryptophyceae	Phytoplankton	1.0	Extinct	Trophic cascade -	Trophic cascade -	Trophic cascade -
Gammaridae	Invertebrate	3.0	Extinct	Predation -	Trophic cascade -	Trophic cascade -
Esocidae	Fish	4.4	Non-extinct	Other	Competition -	Competition -
Salmonidae	Fish	3.9	Non-extinct	Competition -	Other	Predation -
Lotidae	Fish	3.7	Non-extinct	Competition -	Competition -	Predation -
Cyprinidae	Fish	3.6	Non-extinct	Competition -	Competition -	Predation -

Ictaluridae	Fish	3.5	Non-extinct	Competition -	Competition -	Predation -
Percidae	Fish	3.7	Non-extinct	Competition -	Predation -	Predation -
Cottidae	Fish	3.3	Non-extinct	Other	Predation -	Predation -
Astacidae	Invertebrate	3.1	Non-extinct	Trophic cascade +	Predation -	Predation -
Blenniidae	Fish	3.3	Non-extinct	Predation -	Predation -	Predation -
Centrarchidae	Fish	3.3	Non-extinct	Predation -	Predation -	Predation -
Cambaridae	Invertebrate	3.3	Non-extinct	Predation -	Predation -	Predation -
Dreissenidae	Invertebrate	2.5	Non-extinct	Predation -	Predation -	Trophic cascade -
Coenagrionidae	Invertebrate	3.0	Non-extinct	Predation -	Trophic cascade +	Trophic cascade +
Glossiphoniidae	Invertebrate	3.0	Non-extinct	Predation -	Trophic cascade +	Trophic cascade +
Gomphidae	Invertebrate	3.0	Non-extinct	Predation -	Trophic cascade +	Trophic cascade +
Libellulidae	Invertebrate	3.0	Non-extinct	Predation -	Trophic cascade +	Trophic cascade +
Ephemeridae	Invertebrate	2.5	Non-extinct	Predation -	Trophic cascade -	Trophic cascade +
Crambidae	Invertebrate	2.3	Non-extinct	Predation -	Trophic cascade -	Trophic cascade +
Cercopagididae	Invertebrate	3.1	Non-extinct	Predation -	Trophic cascade +	Trophic cascade -
Leptodoridae	Zooplankton	3.1	Non-extinct	Predation -	Trophic cascade +	Trophic cascade -
Polycentropodidae	Invertebrate	2.5	Non-extinct	Predation -	Trophic cascade -	Trophic cascade -
Physidae	Invertebrate	2.2	Non-extinct	Trophic cascade +	Trophic cascade -	Trophic cascade -
Leptoceridae	Invertebrate	2.4	Non-extinct	Trophic cascade -	Trophic cascade -	Trophic cascade -
Empididae	Invertebrate	2.4	Non-extinct	Trophic cascade +	Trophic cascade +	Trophic cascade +
Ecnomidae	Invertebrate	2.4	Non-extinct	Trophic cascade +	Trophic cascade +	Trophic cascade +
Sphaeriidae	Invertebrate	2.0	Non-extinct	Trophic cascade +	Trophic cascade +	Trophic cascade +
Baetidae	Invertebrate	2.4	Non-extinct	Trophic cascade +	Trophic cascade +	Trophic cascade +

Beraeidae	Invertebrate	2.4	Non-extinct	Trophic cascade +	Trophic cascade +	Trophic cascade +
Psychomiidae	Invertebrate	2.4	Non-extinct	Trophic cascade +	Trophic cascade +	Trophic cascade +
Lymnaeidae	Invertebrate	2.0	Non-extinct	Trophic cascade +	Trophic cascade +	Trophic cascade +
Planorbidae	Invertebrate	2.0	Non-extinct	Trophic cascade +	Trophic cascade +	Trophic cascade +
Valvatidae	Invertebrate	2.0	Non-extinct	Trophic cascade +	Trophic cascade +	Trophic cascade +
Bithyniidae	Invertebrate	2.0	Non-extinct	Trophic cascade +	Trophic cascade +	Trophic cascade +
Caenidae	Invertebrate	2.4	Non-extinct	Trophic cascade +	Trophic cascade +	Trophic cascade +
Hydroptilidae	Invertebrate	2.3	Non-extinct	Trophic cascade +	Trophic cascade +	Trophic cascade +
Tateidae	Invertebrate	2.0	Non-extinct	Trophic cascade +	Trophic cascade +	Trophic cascade +
Daphniidae	Zooplankton	2.3	Non-extinct	Trophic cascade +	Trophic cascade +	Trophic cascade -
Chrysophyceae	Phytobenthos	1.0	Non-extinct	Trophic cascade +	Trophic cascade -	Trophic cascade -
Chrysophyceae	Phytoplankton	1.0	Non-extinct	Trophic cascade -	Trophic cascade -	Trophic cascade -
Diatoms	Phytoplankton	1.0	Non-extinct	Trophic cascade +	Trophic cascade +	Trophic cascade -
Dinophyceae	Phytoplankton	1.0	Non-extinct	Trophic cascade +	Trophic cascade +	Trophic cascade -
Chlorophyceae	Phytobenthos	1.0	Non-extinct	Trophic cascade +	Trophic cascade -	Trophic cascade -
Chlorophycceae	Phytoplankton	1.0	Non-extinct	Trophic cascade -	Trophic cascade -	Trophic cascade -
Diatoms	Phytobenthos	1.0	Non-extinct	Trophic cascade +	Trophic cascade -	Trophic cascade -

Part 6. Interaction strengths in the food-web.

Table S4: Average interaction strengths found for consumers with and without different body size of *S. glanis*.

Scenario	**Average interaction strength ±SD (min – max)**
No *S. glanis*	$2.02\ 10^{-3}$ ±2.9510^{-3} ($5.26\ 10^{-6}$ – $1.39\ 10^{-2}$)
S. glanis of 40 cm	$1.96\ 10^{-3}$ ±2.9310^{-3} ($5.26\ 10^{-6}$ – $1.39\ 10^{-2}$)
S. glanis of 85 cm	$1.99\ 10^{-3}$ ±$2.94\ 10^{-3}$ ($5.26\ 10^{-6}$ – $1.39\ 10^{-2}$)
S. glanis of 150 cm	$1.98\ 10^{-3}$ ±2.9310^{-3} ($2.69\ 10^{-6}$ – $1.39\ 10^{-2}$)

Literature cited in supplementary information:

Brose, U. (2010). Body-mass constraints on foraging behaviour determine population and food-web dynamics. *Functional Ecology*, 24, 28-34.

Brose, U., Williams, R.J. & Martinez, N.D. (2006). Allometric scaling enhances stability in complex food-webs. *Ecol. Lett.*, 9, 1228-1236.

Brown, J.H., Gillooly, J.F., Allen A. P., Savage, V.M. & West, G.B. (2004). Toward a metabolic theory of ecology. *Ecology*, 85, 1771–1789.

DeLong, J.P., Okie, J.G., Moses, M.E., Sibly, R.M. & Brown, J.H. (2010). Shifts in metabolic scaling, production, and efficiency across major evolutionary transitions of life. *Proc Natl Acad Sci U S A*, 107, 12941-12945.

Flynn, K.J. & Raven, J.A. (2017). What is the limit for photoautotrophic plankton growth rates? *Journal of Plankton Research*, 39, 13-22.

Hansson, L.-A., Tranvik, L-J. (1996). Quantification of invertebrate predation and herbivory in food chains of low complexity. *Oecologia*, 108, 542-551.

Jacobsen, D., Kaj, S-J. (1994). Invertebrate herbivory on the submerged macrophyte Potamogeton perfoliatus in a Danish stream. *Freshwater Biology* 31, 43-52.

Kalinkat, G., Schneider, F.D., Digel, C., Guill, C., Rall, B.C. & Brose, U. (2013). Body masses, functional responses and predator-prey stability. *Ecol Lett*, 16, 1126-1134.

Kiørboe, T., Saiz, E., Tiselius, P. & Andersen, K.H. (2017). Adaptive feeding behavior and functional responses in zooplankton. *Limnology and Oceanography*, 63, 308-321.

Koen-Alonso, M. (2007). A process-oriented approach to the multispecies functional response. In: *From Energetics to Ecosystems: The Dynamics and Structure of EcologicalSystems* (ed. Rooney, N, McCann, K.S., Noakes, D.L.G.). Springer Netherlands, pp. 1-36.

Makarieva, A.M., Gorshkova, V.G., Li, B.L., Chownc, S.L., Reichd, P.B. & Gavrilove, V.M. (2008). Mean mass-specific metabolic rates are strikingly similar across life's major domains: Evidence for life's metabolic optimum. *PNAS*, 105, 16994-16999.

Yoon, R. J., Williams, E., Levine, S., Yoon, J., Dunne, J., & Martinez, N. D. (2004). Webs on the web (wow): 3D visualization of ecological networks on the www for collaborative research and education. *Proceedings of the IS&T/SPIE Symposium on Electronic Imaging, Visualization and Data Analysis, 5295*, 124-132.