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**Author(s):** Kuparinen, Anna; Uusi-Heikkilä, Silva; Perälä, Tommi; Ercoli, Fabio; Eloranta, Antti P.; Cremona, Fabien; Nöges, Peeter; Laas, Alo; Nöges, Tiina

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## RESEARCH NOTE

# Generalist invasion in a complex lake food web

Anna Kuparinen<sup>1</sup>  | Silva Uusi-Heikkilä<sup>1</sup>  | Tommi Perälä<sup>1</sup>  |  
 Fabio Ercoli<sup>1,2</sup>  | Antti P. Eloranta<sup>1</sup>  | Fabien Cremona<sup>2</sup>  |  
 Peeter Nõges<sup>2</sup>  | Alo Laas<sup>2</sup>  | Tiina Nõges<sup>2</sup> 

<sup>1</sup>Department of Biological and Environmental Science, University of Jyväskylä, Survantie 9 C (Ambiotica), Jyväskylä 40500, Finland

<sup>2</sup>Chair of Hydrobiology and Fishery, Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Kreutzwaldi 5D, Tartu 51006, Estonia

**Correspondence**

Anna Kuparinen, Department of Biological and Environmental Science, University of Jyväskylä, Survantie 9 C (Ambiotica), Jyväskylä 40500, Finland.  
 Email: [anna.k.kuparinen@jyu.fi](mailto:anna.k.kuparinen@jyu.fi)

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**Abstract**

Invasive species constitute a threat not only to native populations but also to the structure and functioning of entire food webs. Despite being considered as a global problem, only a small number of studies have quantitatively predicted the food web-level consequences of invasions. Here, we use an allometric trophic network model parameterized using empirical data on species body masses and feeding interactions to predict the effects of a possible invasion of Amur sleeper (*Perccottus glenii*), on a well-studied lake ecosystem. We show that the modeled establishment of Amur sleeper decreased the biomasses of top predator fishes by about 10%–19%. These reductions were largely explained by increased larval competition for food and Amur sleeper predation on fish larvae. In contrast, biomasses of less valued fish of lower trophic positions increased by about 0.4%–9% owing to reduced predation pressure by top piscivores. The predicted impact of Amur sleeper establishment on the biomasses of native fish species vastly exceeded the impacts of current-day fishing pressures.

**KEYWORDS**

feeding interactions, food webs, invasive species, lake ecosystem, predator–prey interactions, species introduction, trophic interactions

## 1 | INTRODUCTION

Species range shifts due to rapidly changing environmental conditions, traffic by land and water, and intentional species introductions lead to frequent establishments of non-native species in ecosystems (Ricciardi, 2007). Aquatic systems are particularly vulnerable to introductions of alien species, the establishment of which can

cause habitat degradation and loss of native fauna (Rahel, 2002; Havel et al., 2015). For example, the North Sea fish community is becoming increasingly dominated by more southern species due to increasing sea-surface temperatures (Perry et al., 2015). Similarly, cargo ships act as a major vector for the introduction of non-native species in marine and freshwater environments (Ricciardi & MacIsaac, 2022; Sardain et al., 2019).

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Invasion of non-native species is a threat to natural populations and ecosystems, not only by affecting competition among species but also by re-structuring food webs and altering ecosystem functions and ecosystem services (e.g., Havel et al., 2015; Strayer et al., 2006). For example, in the freshwater realm, the invasive Zebra mussel (*Dreissena polymorpha*) has been predicted to affect the whole lake ecosystem functioning and fish community, with potential impacts on commercial fishery (Jaeger Miehl et al., 2009). To better evaluate the ecosystem consequences of invasions followed by non-native species establishment, a synergistic approach coupling invasion and network sciences has recently been proposed (Hui & Richardson, 2019).

Amur sleeper (*Perccottus glenii*) is considered one of the most successful invasive fish species owing to the unprecedented expansion westwards from its natural habitats in the east region of Eurasia in Russia, north-eastern China, and northern North Korea (Copp et al., 2005; Reshetnikov, 2010; Reshetnikov et al., 2017). Amur sleeper was originally intentionally introduced to the western parts of Eurasia as a baitfish (Reshetnikov, 2004). Today, the species is widespread in most of the central and eastern Europe (Harka, 1998; Kutsokon et al., 2014; Rechulicz et al., 2015; Reshetnikov & Karyagina, 2015), and its expansion rate is predicted to increase (Reshetnikov & Ficetola, 2011; Vilizzi et al., 2019). Early age-at-maturity and prolonged spawning period (Nyeste et al., 2017), ability to settle at high abundances in even adverse habitats (Reshetnikov, 2003), and a generalist feeding strategy (Grabowska et al., 2009) make Amur sleeper an efficient freshwater invader. For these reasons, Amur sleeper is an ideal species to study rapid invasions in aquatic ecosystems (Reshetnikov, 2013).

Here, we couple an allometric trophic network (ATN) model (Boit et al., 2012; Kuparinen et al., 2016), which describes the bioenergetic dynamics of an aquatic food web, with detailed empirical data on Amur sleeper life-history and diet to evaluate how the successful establishment of the species may alter the dynamics of a natural lake food web. We do this by investigating the community-level consequences of Amur sleeper invasion using Lake Võrtsjärv (LV) in Estonia as our study system (the characteristics of LV and its food web are presented in Appendix S1). LV forms an ideal system for our study objectives as this freshwater ecosystem has been extensively studied for more than six decades and its complex food-web structure has been resolved (Nõges et al., 1998; Cremona et al., 2018; Figure 1). Most importantly, Amur sleeper has not yet been detected in LV, although observations of its establishment and breeding have been made in the Narva Reservoir connected to LV by two rivers, as well as in its nearby waterbodies (Rau et al., 2017). Thus,

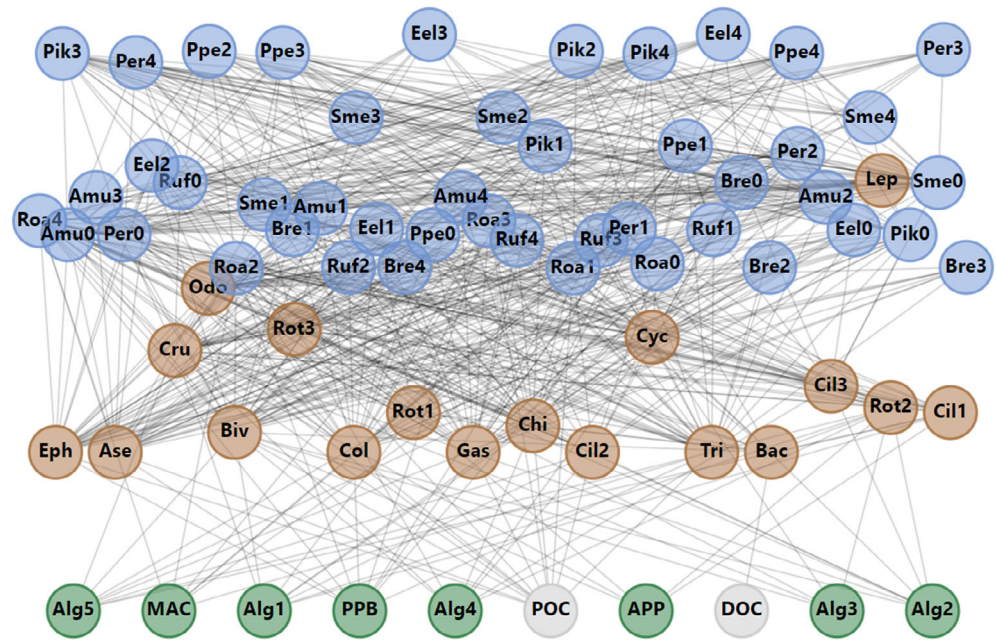
LV is at a high risk to experience Amur sleeper invasion in the near future. These properties of LV coupled with the complex ATN model of food-web dynamics facilitate mechanistic, comparative predictions of how Amur sleeper invasion might alter the LV ecosystem, change conservational statuses of the native species, affect local fisheries and other ecosystem services provided by the second largest lake within the Baltic countries.

## 2 | MATERIALS AND METHODS

We used an ATN model (Boit et al., 2012; Kuparinen et al., 2016) to predict the food web-level consequences of Amur sleeper's invasion into LV. We utilized information about the LV fish community and the food-web structure (Ojaveer et al., 2003; Tables 1 and 2; Appendix S1). To predict how the establishment of Amur sleeper might change the LV food-web structure, we analyzed Amur sleeper's diet based on stomach contents in other waterbodies within 200 km from LV where the species has been established. Individuals ( $n = 66$ ; ages range from 0+ to 4+ years) were sampled during the summer 2018 by electrofishing in three different sites in Narva Reservoir, as well as in a semiconnected pond and outflow cooling system channel. Except for the channel, the sampling sites were similar to the littoral vegetated habitats in LV with muddy and sandy bottoms. Prey items in Amur sleeper foreguts consisted of terrestrial detritus, aquatic plants, macroinvertebrates, and fish (Figure S1). These data were used as the basis for the choice of the Amur sleeper feeding links in the ATN model (Table 2). As the foregut contents varied among sites and individuals, the data did not provide any support for differential prey item preference by Amur sleeper but rather reflected varying prey availability. Consequently, our ATN model assumes equal prey preferences treating feeding links equally, such that realized consumption depends on the relative prey species abundances and the feeding-link specific parameters of the functional response in the model.

The LV food web was structured into six groups: primary producers, heterotrophic bacteria, ciliates, zooplankton, benthic macroinvertebrates, and fish (Heberman et al., 2004; Nõges et al., 1998). Each group was further divided into main guilds according to their carbon body mass, functional feeding groups, and age-classes (fishes). LV food web was described through 68/73 nodes and 611/710 links without/with Amur sleeper, respectively, the former corresponding to functional guilds and the latter to their feeding interactions (Figure 1, Table 2). Ecological functionality of the nodes was described by their intrinsic growth (producers) and metabolic rates (consumers)

**FIGURE 1** Lake Vörtsjärv food web. Nodes describe functional guilds or age-classes of fishes and links among nodes describe feeding interactions. Producers, invertebrates, and fishes are colored with green, brown, and blue, respectively. Particulate and dissolved organic carbon (POC and DOC, respectively) are shown in gray. Guild labels correspond to those given in Table 2.



**TABLE 1** LV fish community. Details of the full LV food web in Table 2, Figure 1, and in Appendix S1.

Fish species	Fishing mortality (%) <sup>a</sup>	Age at maturity (year) <sup>b</sup>
Smelt ( <i>Osmerus eperlanus</i> )	0 <sup>c</sup>	1
Ruffe ( <i>Gymnocephalus cernua</i> )	5.2	1
Roach ( <i>Rutilus rutilus</i> )	5.7	2
Bream ( <i>Abramis brama</i> )	3.8	2
Perch ( <i>Perca fluviatilis</i> )	8.1	3
Eel ( <i>Anguilla anguilla</i> )	14.3	-
Pikeperch ( <i>Sander lucioperca</i> )	4	3
Pike ( <i>Esox lucius</i> )	22.5	2
Amur sleeper ( <i>Perccottus glenii</i> )	0	1

<sup>a</sup>Nonzero fishing mortalities estimated by Cremona et al. (2018).

<sup>b</sup>In the first year of maturity, 50% of the age class was assumed mature, whereas in the following years the fraction of mature individuals was assumed 100%.

<sup>c</sup>No commercial smelt fishery.

calculated through allometric scaling by body mass (Brose et al., 2006) and their feeding links (Table 2). Feeding link-specific parameters of the functional response were determined as described by Bland et al. (2019, app. S1), with the exception of treating fish larvae as invertebrates and including feeding links to the detritus. See Table 2 and Appendix S1 for further details about individual body masses, guild-specific diets, and feeding parameters.

The biomass density (units in micrograms of carbon per cubic meter of water; hereafter ‘biomass’) dynamics

of the LV food web were simulated following the ATN model described by Boit et al. (2012) and further expanded by fish life-history dynamics by Kuparinen et al. (2016, see app. S1). In this model, producers grow according to a logistic growth model with a shared community-wide carrying capacity, and feeding interactions among consumers and their resources are described by a hybrid DeAngelis–Beddington–Holling type III functional response. Biomass dynamics were divided into two parts. (i) Within a growing season of 90 days, the biomass dynamics are simulated in continuous time and they consist of the producer intrinsic growth, consumer and fish feeding, maintenance of organisms’ bodily functions, and the allocation of adult fish biomass for reproduction. These dynamics were simulated by solving a set of ordinary differential equations (see Appendix S1). (ii) The dynamics between consecutive growth periods (years) comprises the birth of new fish larvae and fish aging from one age class to the next. Fish species were divided into five age-classes (larvae, juveniles, 2–4+ years). At the end of each growing season, fish biomass shifts from the previous to the following age-class and the adult age-classes (Table 1) invest a portion of their consumption gains to the production of new larvae (penalized under starvation). As the European eel (*Anguilla anguilla*) population in LV is maintained by stocking, eel larvae were annually supplemented by an amount corresponding to the empirically estimated eel stocking intensity in LV (0.25% of eel standing stock biomass, see Appendix S1).

We simulated LV food-web dynamics in the absence and presence of Amur sleeper, to mimic the current situation, where Amur sleeper is not present in LV as well as

TABLE 2 Lake Vörtsjärv food web.

ID	Name	Description	Body Mass <sup>a</sup>	Diet (feeding links)	Trophic position	Intrinsic growth rate/metabolic rate
0	DOC	Dissolved organic matter	n.a.	n.a.		
1	Alg1	Single-cell algae	3.05E-02	n.a.	1.00	1
2	Alg2	Large, single-cell algae or colonies	2.15E-01	n.a.	1.00	0.746
3	Alg3	Filamentous blue and green algae	5.74E-02	n.a.	1.00	0.91
4	Alg4	Diatoms, algal colonies	9.27E-01	n.a.	1.00	0.599
5	Alg5	Small, coccal algae	9.78E-03	n.a.	1.00	1.186
6	APP	Autotrophic picoplankton	1.13E-04	n.a.	1.00	2.316
7	PPB	Biofilm ( $\mu\text{gC per m}^2$ ) <sup>b</sup>	8.90E+02	n.a.	1.00	0.25
8	POC	Settled/sedimented/suspended detritus	n.a.	n.a.		
9	MAC	Macrophytes	9.59E+06	n.a.	1.00	0.062
10	Bac	Heterotrophic bacteria	5.60E-07	0	1.00	0.04
11	Cil1	Small ciliates <20–50 $\mu\text{m}$	2.29E-03	1, 5–6, 10	2.00	0.463
12	Cil2	Medium-size ciliates 50–100 $\mu\text{m}$	2.94E-02	1, 2, 4–5, 8	2.00	0.316
13	Cil3	Larger ciliates >100 $\mu\text{m}$	1.35E-01	2, 4, 11	2.00	0.251
14	Rot1	Small rotifers	1.16E-03	1, 5–6, 10	2.00	0.513
15	Rot2	Medium-size rotifers	4.25E-02	1–6, 10–11	2.13	0.299
16	Rot3	Large rotifers	2.82E+00	2–4, 11–15	2.70	0.159
17	Cru	Mostly cladocerans	5.42E-01	1–6, 8, 10–16	2.54	0.204
18	Cyc	Cyclopoid copepods	7.92E-01	1–5, 11–16	2.64	0.192
19	Lep	Large, carnivorous cladocerans	8.19E+00	16–18	3.60	0.136
20	Eph	Caenis sp. collector	9.71E+01	7–8	2.00	0.094
21	Cru	Asellus aquaticus collector/shredder	5.29E+02	7–8	2.00	0.073
22	Gas	Gastropoda grazer	1.60E+03	7–8	2.00	0.062
23	Chi	Chironomus plumosus	1.50E+02	1–2, 4–5, 8, 10	2.00	0.088
24	Tri	Trichoptera shredder/collector	9.48E+02	7–9	2.00	0.067
25	Col	Coleoptera scrapers/collectors/gatherers	1.38E+02	7–9	2.00	0.089
26	Biv	Bivalvia (Pisidium) filterers	1.68E+02	1–6, 8, 10	2.00	0.086
27	Odo	Odonata predator	2.02E+03	20–21, 23–25	3.00	0.06
28	Sme0 (0+ – 1 year)	Smelt larvae	1.18E+01	12–13, 17–19	3.70	0.2143
29	Roa0 (0+ – 1 year)	Roach larvae	7.38E+04	7–10, 12–13, 17–19	3.19	0.1955
30	Bre0 (0+ – 1 yr)	Bream larvae	2.76E+05	12–13, 17–19	3.70	0.1554
31	Ruf0 (0+ – 1 yr)	Ruffe larvae	8.37E+04	12–13, 17–19	3.70	0.1868
32	Per0 (0+ – 1 yr)	Perch larvae	1.57E+05	12–13, 17–27	3.37	0.1637
33	Eel0 (0+ – 1 yr)	Eel larvae	4.08E+05	13, 17–27	3.40	0.1467
34	Ppe0 (0+ – 1 yr)	Pike-perch larvae	1.57E+06	12–13, 17–27	3.37	0.1293
35	Pik0 (0+ – 1 yr)	Pike larvae	4.33E+06	12–13, 17–27	3.37	0.1505
36	Amu0 (0+ – 1 yr)	Amur sleeper larvae	3.74E+04	12–13, 17–27	3.37	0.1969
37	Sme1 (1–2 years)	Smelt	2.46E+05	11–19	3.56	0.148
38	Roa1 (1–2 years)	Roach	4.18E+05	7–27	3.16	0.1566
39	Bre1 (1–2 years)	Bream	1.51E+06	13, 17–27	3.40	0.1317
40	Ruf1 (1–2 years)	Ruffe	3.49E+05	13, 17–27	3.40	0.1594

TABLE 2 (Continued)

ID	Name	Description	Body Mass <sup>a</sup>	Diet (feeding links)	Trophic position	Intrinsic growth rate/metabolic rate
41	Per1 (1–2 years)	Perch	9.45E+05	14–27	3.41	0.1401
42	Eel1 (1–2 years)	Eel	1.77E+06	14–27	3.41	0.1281
43	Ppe1 (1–2 years)	Pike-perch	7.23E+06	20–32, 34–38, 40–41	3.93	0.1102
44	Pik1 (1–2 years)	Pike	1.47E+07	20–32, 34–38, 40–41	3.93	0.1083
45	Amu1 (1–2 years)	Amur sleeper	4.57E+05	20–29, 31	3.54	0.1583
46	Sme2 (2–3 years)	Smelt	3.94E+05	16–19, 28	4.11	0.1167
47	Roa2 (2–3 years)	Roach	8.86E+05	7–27	3.16	0.1412
48	Bre2 (2–3 years)	Bream	6.30E+06	20–27	3.17	0.1126
49	Ruf2 (2–3 years)	Ruffe	6.25E+05	20–27	3.17	0.1453
50	Per2 (2–3 years)	Perch	2.26E+06	17–32, 36–38, 45	3.88	0.1304
51	Eel2 (2–3 years)	Eel	4.53E+06	20–29, 31–32, 36–38, 45	3.81	0.1134
52	Ppe2 (2–3 years)	Pike-perch	2.12E+07	28–32, 34–38, 40–41, 45–47, 49, 55, 64	4.53	0.098
53	Pik2 (2–3 years)	Pike	3.12E+07	28–32, 34–38, 40–41, 45–47, 49, 55, 64	4.53	0.0962
54	Amu2 (2–3 years)	Amur sleeper	1.64E+06	20–29, 31, 36	3.61	0.1369
55	Sme3 (3–4 years)	Smelt	3.94E+05	16–19, 28	4.11	0.1167
56	Roa3 (3–4 years)	Roach	1.72E+06	7–32, 36	3.46	0.1304
57	Bre3 (3–4 years)	Bream	1.39E+07	20–27	3.17	0.1026
58	Ruf3 (3–4 years)	Ruffe	8.51E+05	20–28	3.34	0.1427
59	Per3 (3–4 years)	Perch	4.58E+06	28–32, 36–38, 45–46	4.54	0.1168
60	Eel3 (3–4 years)	Eel	9.05E+06	28–32, 36–38, 45–46, 54–55, 64	4.63	0.1033
61	Ppe3 (3–4 years)	Pike-perch	5.62E+07	28–32, 34–38, 40–41, 45–47, 49, 54–56, 58, 64	4.52	0.0885
62	Pik3 (3–4 years)	Pike	5.68E+07	28–38, 40–41, 45–47, 49, 54–56, 58, 64	4.51	0.0888
63	Amu3 (3–4 years)	Amur sleeper	3.25E+06	20–29, 31, 36	3.61	0.1265
64	Sme4 (4+ years)	Smelt	3.94E+05	16–19, 28	4.11	0.1167
65	Roa4 (4+ years)	Roach	2.95E+06	7–32, 36	3.46	0.1215
66	Bre4 (4+ years)	Bream	2.39E+07	20–27	3.17	0.097
67	Ruf4 (4+ years)	Ruffe	1.33E+06	20–28	3.34	0.1323
68	Per4 (4+ years)	Perch	1.21E+07	28–41, 45–47, 49, 54, 56	4.46	0.1058
69	Eel4 (4+ years)	Eel	1.64E+07	28–32, 36–38, 45–46, 54–55, 64	4.63	0.0961

(Continues)

TABLE 2 (Continued)

ID	Name	Description	Body Mass <sup>a</sup>	Diet (feeding links)	Trophic position	Intrinsic growth rate/metabolic rate
70	Ppe4 (4+ years)	Pike-perch	1.16E+08	28–32, 34–38, 40–41, 45–47, 49, 54–56, 58, 63–65, 67, 72	4.52	0.0818
71	Pik4 (4+ years)	Pike	8.30E+07	28–38, 40–41, 45–47, 49, 54–56, 58, 63–65, 67, 72	4.51	0.0847
72	Amu4 (4+ years)	Amur sleeper	5.87E+06	20–29, 31, 36	3.61	0.1164

<sup>a</sup>In µgC.

<sup>b</sup>Based on *Myriophyllum spicatum* standing stock biomass µgC per m<sup>2</sup>.

the future scenario when Amur sleeper has successfully invaded and established in LV, respectively. To investigate whether the consequences of Amur sleeper establishment were provisional to anthropogenic impacts, we carried out simulations both in pristine conditions and when fish species were exposed to their current levels of fishing mortality (Table 1). Simulations consisted of an initial burn-in period, pristine equilibrium conditions, a fishing burn-in period, and fishing equilibrium conditions, each of which lasted for 50 years. The burn-in periods were chosen so that the system had enough time to settle at its equilibrium states. We then compared relative changes in the guild/species specific biomasses, and biomass gains from feeding both in the presence and absence of Amur sleeper, during pristine and fished conditions.

Simulations were performed in Matlab (2021) and their results were visualized in R (R Core Team, 2021).

### 3 | RESULTS

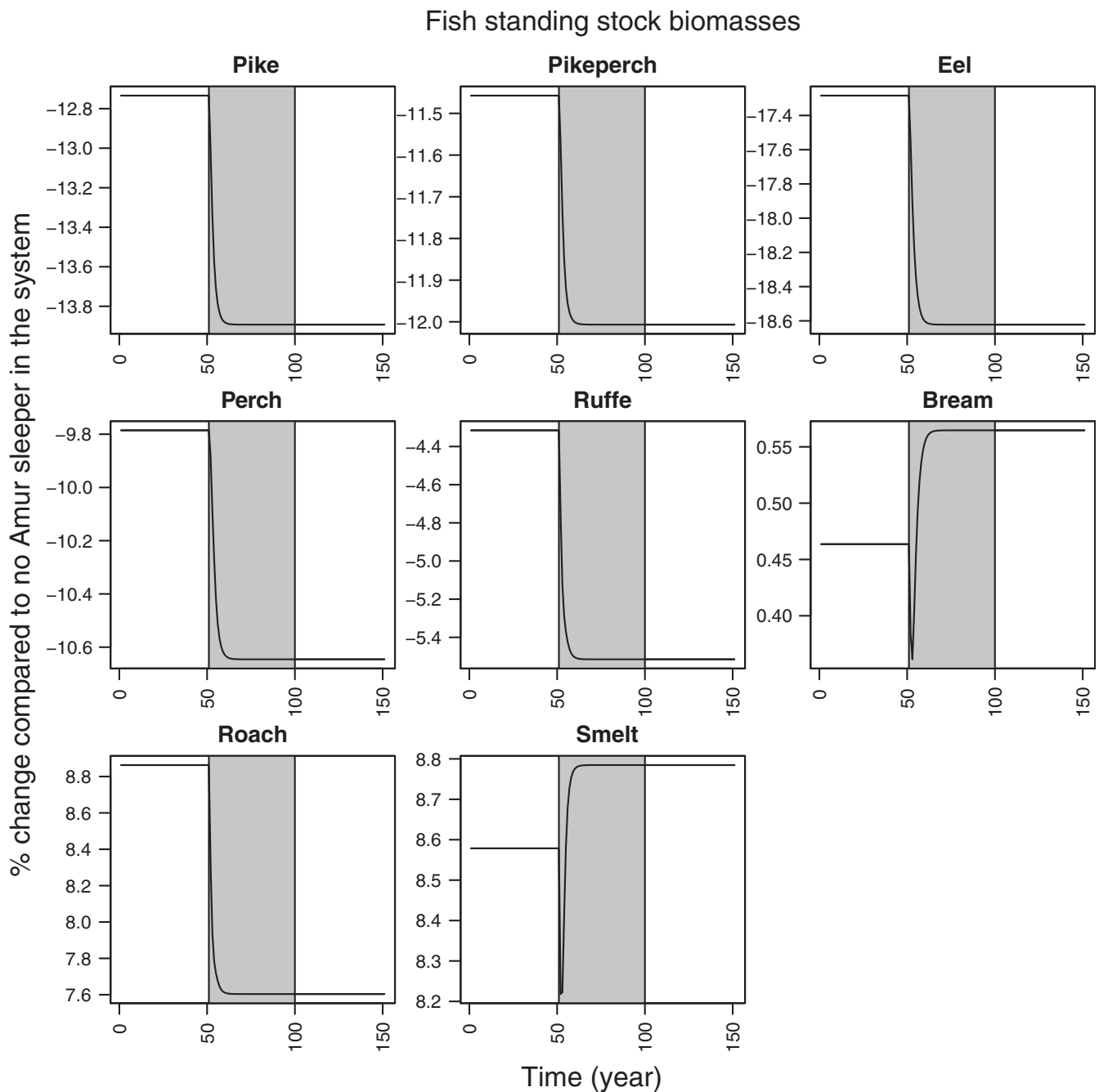
Based on the ATN model predictions, the establishment of Amur sleeper in LV reduced the biomasses of top predator fishes but slightly increased or had no effect on fishes at lower trophic positions. The biomasses of piscivores, such as pike (*Esox lucius*), pikeperch (*Sander lucio-perca*) and perch (*Perca fluviatilis*), were reduced by 9.8%–13.9% when compared to the food web model without Amur sleeper (Figure 2). Eel, which is particularly valued for fisheries in LV (Kangur et al., 2002), decreased by 17.3%–18.5%. Also, ruffe (*Gymnocephalus cernua*) decreased slightly (by 4.3%–5.5%), whereas bream (*Abramis brama*), roach (*Rutilus rutilus*) and smelt (*Osmerus eperlanus*) increased by 0.4%–8.9%. Among invertebrate

consumers, the establishment of Amur sleeper consistently reduced their standing stock biomasses (Figure 3). Differences between pristine and fished conditions were minor ( $\leq 1.5\%$ ) compared to the overall effect of Amur sleeper establishment (Figures 2 and 3). Amur sleeper itself established in LV at abundances of 6.6% and 5.8% of the total fish biomass, in the presence and absence of fishing, respectively. The other fish biomasses were as follows (% of total fish biomass), with/without fishing, respectively: pike 12.6%/15.3%; pikeperch 15.3%/14.5%; eel 16.5%/18.1%; perch 9.5%/9.3%; ruffe 4.9%/4.6%; bream 6.8%/6.5%; roach 20.7%/19.4%; smelt 7.1%/6.5%.

Biomass gains by feeding declined in six out of eight fish species in the presence of Amur sleeper (Figures S3–S11). The changes in fish standing stock biomasses reflect the balance between reduced feeding, fish larvae predation by Amur sleeper, and reduced predation pressure by top piscivores. Overall, the establishment of Amur sleeper into LV reduced average biomasses throughout the trophic positions (Figure S2).

### 4 | DISCUSSION

The present study illustrates that the establishment of a generalist fish in the studied LV system can reduce the biomasses of native top predatory fishes (Figure 2). The greatest losses are predicted to occur for species that are most valued by fishermen, namely, eel, pike, and pikeperch. This would directly reduce the value of ecosystem services provided by the lake, such as recreational and commercial fishing (Pejchar & Mooney, 2009). On the other hand, the resulting increase of less valuable fishes may magnify the predation pressure on macroinvertebrates and also the resuspension of silt, nutrients,



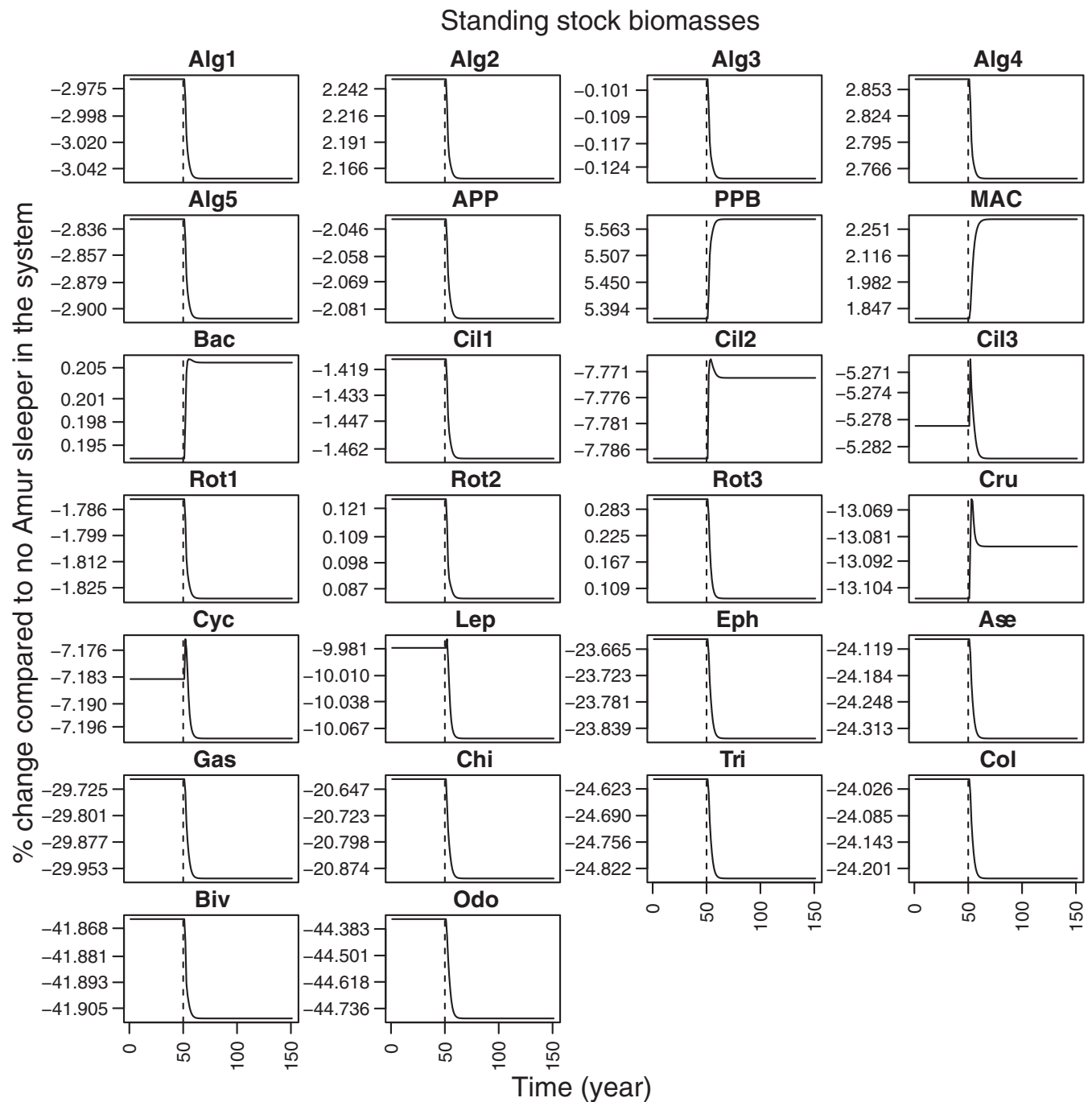
**FIGURE 2** Relative changes in fish biomasses after the invasion of Amur sleeper to LV. Panels show the biomass for each fish species in the absence (years 0–50) and presence of fishing (years 101–150). Burn-in period from unfished to fished system (years 51–100) is shaded in gray.

pollutants, and methane from the sediment due to increased bioturbation (Kristensen et al., 2012). These predictions suggest that Amur sleeper invasion to LV is likely to adversely affect both the fisheries and the abiotic environment in the lake. Given that Amur sleeper has already been detected in the waterbodies connected to LV (Reshetnikov, 2010), preventing the invasion may no longer be possible, but mechanistic understanding of its

consequences might nonetheless help to mitigate some of the potential negative impacts.

Our study highlights some of the factors underlying an impactful establishment, such as the high number of interactions between the alien and resident species and the omnivorousness of the alien species (Hui & Richardson, 2019). Amur sleeper's diet is broad (11–13 links per age class) and covers a range of trophic





**FIGURE 3** Relative changes in the non-fish species (Table 2) biomasses in the absence (years 0–50) and presence (years 101–150) of fishing. The beginning of fishing is denoted with a vertical line.

positions from herbivores to fish larvae (Table 2; Figure 1). Besides stressing these structural properties of the food web facilitating Amur sleeper establishment, the present study also identifies the feedback loops through which the establishment of the alien species affects the food-web dynamics and predicts the changes in the biomasses of the resident species:

- i. Although Amur sleeper may settle into the LV ecosystem at relatively low abundances compared to other fish species, its impacts on the top predators can be substantial (Figure 2) due to predation on fish larvae and eggs. This effect of Amur sleeper on the native fish community structure has also been detected in other lakes invaded by Amur sleeper

- (Kati et al., 2015; Litvinov & O'Gorman, 1996). Moreover, Rakauskas et al. (2019) found that in four lakes highly invaded by Amur sleeper (66%–95% of the total fish biomass) top piscivore catches were negligible, suggesting that the population abundances were very low. Our predictions are also well in line with the meta-analysis by Gallardo et al. (2016), who found that a piscivore invader causes large reductions in native fish abundances.
- ii. While the impacts of non-native species have been suggested to depend on human-mediated factors in the recipient ecosystem (Hui & Richardson, 2019), our model predicted that the prevailing fishing pressures had minor effects on the ecosystem compared to the effect of the Amur sleeper establishment, as the differences between biomasses with or without fishing were <1.5%. However, it should be noted that the potential impacts of Amur sleeper establishment may also interact with other human activities, such as the stocking of native species. Also, changes in water quality and in the intensity of fishing combined with the establishment of the invasive species may induce further changes in the structure and function of the lake food web (Dunlop et al., 2019; Vander Zanden et al., 1999). Hence, the successful prevention and mitigation of the potential impacts of Amur sleeper invasion and establishment in LV demand both monitoring and holistic understanding of the species and the anthropogenic stressors in the recipient ecosystem (Gozlan et al., 2010).

While we used a novel network approach to investigate the consequences of successful invasion, there are also limitations. As with any modeling study, it remains unclear how well the model represents the natural system. However, the applied ATN model has been empirically validated by Boit et al. (2012) for the dynamics of Lake Constance pelagic plankton community, and thus it can provide reasonable predictions for biomass flows in size-structured aquatic food webs. To limit the number of assumptions made, we did not focus on how the impacts of the invasion initially propagate in the food web, but rather compare the current state of LV system to the state where Amur sleeper has already established a self-sustaining population. We also ignore the long-term eco-evolutionary feedback loops, which might further modify the recipient ecosystem structure and function (Strayer et al., 2006). The eco-evolutionary perspective certainly warrants for further research once the methodology becomes available (Hui & Richardson, 2019; Perälä & Kuparinen, 2020). Nonetheless, our predictions about the future changes in the LV fish community based on the effects of Amur sleeper alone can be viewed as

conservative, as consequences of similar magnitude have also been predicted to result from climate change and eutrophication (Moss et al., 2011), which currently affect LV (Cremona et al., 2017), but are not accounted for by our ATN model.

While Amur sleeper is efficient at utilizing various food resources ranging from ciliates to vertebrates, and can thus avoid competition with other species, there are also additional pathways through which it can affect the ecosystem: Amur sleeper can efficiently escape predation (Kati et al., 2015) making it more resilient than some of its competitors while at the same time it can transmit diseases to other species (Kvach et al., 2020; Pupins et al., 2023). As a generalist intermediate consumer, Amur sleeper can cause significant and hard-to-predict top-down and bottom-up effects in ecosystems it invades (Reshetnikov, 2013). According to our results, Amur sleeper can have a substantial effect on native species in LV. The decreased abundance of top predator fishes and increased abundance of zooplanktivorous fishes may trigger a trophic cascade (Bhele et al., 2022; Ripple et al., 2016) resulting in increased harmful algal blooms (Cremona et al., 2018) and increased water turbidity owing to reduced zooplankton grazing. Due to its ability to become rapidly abundant in invaded habitats (Bogutskaya & Naseka, 2002; Koščo et al., 2003), Amur sleeper may induce harmful bottom-up processes, for example, through bioturbation. Decreased light availability and increased physical disturbances may further limit the growth of benthic macrophytes and periphyton, which are highly important for sediment stability, especially in LV ecosystem characterized by high sediment resuspension, and also for providing food and shelter for diverse fauna (Jeppesen et al., 1998). These processes imply that Amur sleeper may become a key ecosystem engineer (Wright & Jones, 2006) that modifies the abiotic and biotic conditions in invaded systems. To mitigate these effects, Litvinov and O'Gorman (1996) stress the importance to maintain piscivorous fish populations to control the Amur sleeper population. Rakauskas et al. (2019) found that the reintroduction of native piscivorous pike and perch can be a successful biocontrol method to suppress Amur sleeper populations in invaded eutrophic lakes. Nonetheless, in one out of the four studied lakes even after a drastic reduction of Amur sleeper abundance (from 97% to 1.9% of total fish biomass), the Amur sleeper population was still able to survive, reach the age of maturity and re-establish its population (Rakauskas et al., 2019).

Implementations of network approaches to species invasion projections remain scarce and mark a novel avenue of invasion biology research (Hui & Richardson, 2019). Such a paradigm shift in the invasion biology

requires further development of the theory, methodology and case-studies. Our study provides quantitative predictions for the ecosystem-level impacts of a generalist species establishment. While identifying potential effects of Amur sleeper invasion on the LV food web, our study highlights the power of considering food-web processes in the management and mitigation of human impacts in aquatic ecosystems subject to multiple stressors (Harvey et al., 2017; Kovalenko, 2019; Romanuk et al., 2009).

### AUTHOR CONTRIBUTIONS

Anna Kuparinen and Fabio Ercoli developed the study idea; Fabio Ercoli collected samples; all the authors participated in the model parameterization, Tommi Perälä, and Anna Kuparinen run the simulations and analyzed the results; Anna Kuparinen wrote the initial draft; all authors participated finalizing the manuscript.

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### DATA AVAILABILITY STATEMENT

Codes and simulation data are available in Dryad: <https://doi.org/10.5061/dryad.z34tmpgk2>

### ORCID

Anna Kuparinen  <https://orcid.org/0000-0002-7807-8946>

Silva Uusi-Heikkilä  <https://orcid.org/0000-0001-6503-455X>

Tommi Perälä  <https://orcid.org/0000-0002-4995-5997>

Fabio Ercoli  <https://orcid.org/0000-0003-2433-6222>

Antti P. Eloranta  <https://orcid.org/0000-0002-8893-0135>

Fabien Cremona  <https://orcid.org/0000-0002-0559-6259>

Peeter Nöges  <https://orcid.org/0000-0003-2919-6038>

Alo Laas  <https://orcid.org/0000-0002-4801-0377>

Tiina Nöges  <https://orcid.org/0000-0002-4558-7373>

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