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Impacts of the accumulated extinction of endangered species on stream food webs

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ABSTRACT

The world is facing a serious biodiversity-loss crisis and stream ecosystems are among the most vulnerable. Human-induced disturbances are accelerating the loss of stream biodiversity; however, their ecological impacts are poorly understood. Here, we comprehensively investigated the impact of biodiversity loss on stream food webs using massive food web data (> 1 300 webs). We analyzed the structural changes of food webs upon accumulation of biodiversity loss and specifically compared the severity of losses between fish or benthic macroinvertebrates. In particular, we focused on currently threatened and near-threatened species, to reflect realistic extinction. We simulated their sequential and accumulative extinctions and analyzed the changes in food web structural indices using a linear mixed effect model. Stream food webs tended to be robust against the loss of threatened species; however, the accumulated extinction, including both threatened and near-threatened species, caused substantial changes in food web structures. Notably, significant decreases in the number of links, link density, and generality were observed, indicating the vulnerability of the system. The loss of fish caused larger changes in the food web structure compared to that of benthic macroinvertebrates, indicating the relative importance of fish species in sustaining food web structures. Food web alteration may lead to substantial changes in ecosystem functioning. Our study suggests preemptive action to protect near-threatened species as well as threatened ones for conserving stream ecosystems and their services. Furthermore, we suggest that the food web framework is useful for diagnosing ecosystem-level impacts of species loss in biodiversity conservation.

1. Introduction

The world is facing a serious biodiversity-loss crisis (Ceballos et al., 2015). Over 42 000 species are threatened by extinction, representing approximately 28% of all species evaluated by the International Union for Conservation of Nature (IUCN) (IUCN, 2022). More seriously, species extinction can disrupt the structure and function of ecosystems. Historically, overexploitation of marine fisheries has caused the depletion and extinction of aquatic resources, leading to changes in the entire ecosystem structure (Jackson et al., 2001). The collapse of the cod population on the Canadian coast caused changes in the population at lower trophic levels through top-down cascading effects (Frank et al., 2005). There is a consensus on the seriousness of species extinction or its subsequent impacts

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(Cardinale et al., 2012); however, the current biodiversity loss is unprecedentedly large and rapid, and its consequences remain unknown. Therefore, more research is required to reveal the ecological impacts of ongoing biodiversity loss, which will be critical for conserving biodiversity and ecosystems.

Stream ecosystems are among the most vulnerable ecosystems. Various factors, including habitat degradation, urban and road expansion, pollution, exotic species, and waterway construction, have accelerated biodiversity loss in stream ecosystems (Reid et al., 2019). A food web is vital in stream ecosystems because it plays an important role in sustaining many stream functions and services, such as primary production, respiration, and decomposition, as well as in transferring energy and nutrients from bottom to top species (Petchey et al., 1999; Thompson et al., 2012). Loss of biodiversity can lead to changes in stream food webs by affecting associated species through trophic chains, which may subsequently alter stream functions and services (Donohue et al., 2017; Petchey et al., 2004). Therefore, understanding food webs is critical to reveal and predict changes in stream ecosystems following biodiversity loss (Keyes et al., 2021; Woodward, 2009). Species manipulation experiments, which typically remove one or a few species or control their abundance, have been conducted to examine the effects of species extinction on food webs (Donohue et al., 2017; Romo et al., 2004). Many studies have revealed that biodiversity loss hinders ecosystem functions such as production, decomposition, and nutrient recycling (Romo et al., 2004; Wojdak, 2005). However, these experiments are usually limited to small-scale food webs mainly composed of three or four species and conducted under controlled laboratory conditions. This may be insufficient to fully represent the response of complex food webs in real ecosystems to ongoing biodiversity loss (Schiesari et al., 2009). The impact of stream biodiversity loss remains unclear, and a large-scale systematic understanding is required (Brose et al., 2017; Harvey et al., 2017).

Food web researchers have traditionally explored the effects of species extinction on ecosystems using species removal simulations (Dunne et al., 2002). Species removal simulations have been performed based on classical extinction sequences that are derived from network science (i.e., random extinction sequences or sequences from most/least-linked to least/most-linked species) (Dunne et al., 2002). Accordingly, it is well known that food webs tend to be robust against random species removal, which has been explained by the structural characteristics of networks (e.g., degree distribution, nestedness, or connectance) (Dunne et al., 2009; Kaiser-Bunbury et al., 2010; Purvis et al., 2000). This simulated food web framework is useful for detecting and understanding large-scale ecosystem-level changes (Keyes et al., 2021). However, the real-world species extinctions in nature do not occur at random or sequentially in the order of link numbers because species extinction events, especially the human-derived ones, are often selective (Russell et al., 1998). Moreover, the effects of such realistic extinction (hereafter, used conceptually as a counterpart of classical extinction sequences) and its magnitude can be different from those of classical extinction sequences (de Visser et al., 2011; García-Valdés et al., 2018). For instance, plant communities in grassland ecosystems show a greater reduction in plant biomass for random extinctions than for non-random extinctions (Schläpfer et al., 2005). Lake food webs tended to be less sensitive to the realistic extinctions based on a geographically

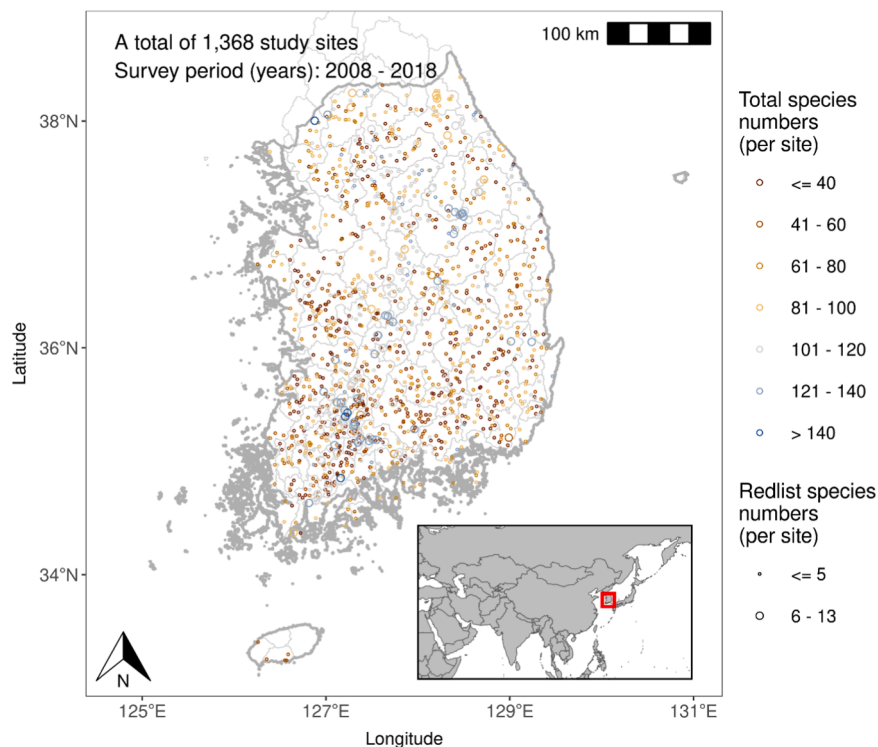


Fig. 1. A total of 1 368 study sites in South Korea were used in this study. Biological survey data obtained from 2008 to 2018 through the National Aquatic Ecological Monitoring Program (NAEMP) were collected for each site where endangered species, reported by the Korean regional Red List, occurred more than once (circles). The colors and sizes of the circles represent the total and Red List species numbers per site, respectively.

nested pattern of species (i.e., less prevalent species were assumed to be extinct first), compared to the results using classical extinction sequences (Srinivasan et al., 2007). From the practical perspective, using realistic extinction sequences that takes into account species traits, extinction probabilities, or conservation status might be a better approach to solving biodiversity loss issues compared to the classical approach; however, related studies are very rare so far (but see de Visser et al., 2011; Srinivasan et al., 2007).

The IUCN Red List of Threatened Species, the most comprehensive species-level assessment system, has evaluated species at high risk of global extinction and has been continuously updated with newly evaluated species (IUCN, 2022). Each taxon was classified into specific categories according to the extinction risk as follows: Extinct (EX), Extinct in the Wild (EW), Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), and Least Concern (LC) (IUCN, 2001). In particular, the three categories, CR, EN, and VU, corresponding to threatened species, were quantitatively evaluated by considering the population size reduction rate and geographical range decline for each species. This study used the IUCN Red List and its categories to simulate a more realistic species extinction and explored the effects of their extinction on stream food webs. Notably, we used a huge amount of the Korean stream food web data (a total of 1 368 food webs, covering diverse scales from small- to large-sized webs), providing a systematic and comprehensive understanding of the impacts of endangered species losses on stream ecosystems. Specifically, we established two hypotheses: (1) stream food webs are severely impacted as the degree of biodiversity loss increases, and (2) extinctions of fish and benthic macroinvertebrates, which have different trophic positions and properties within the food web, have different impacts on food webs. These were tested using a linear mixed effect model by analyzing the impacts of extinction of threatened and near-threatened species on various food web indices. In addition, we simulated random extinctions for comparison with our approach.

2. Material and Methods

2.1. Study sites and data acquisition

South Korea (approximately 37° N, 127° 30' E) is located in East Asia, constituting the southern half of the Korean Peninsula (Fig. 1). Since 2008, the Korean government implemented the National Aquatic Ecological Monitoring Program (NAEMP) to monitor and evaluate the health of domestic rivers and streams (MOE/NIER, 2008). Biological survey data were systematically accumulated through the NAEMP, and criteria and monitoring methods (MOE/NIER, 2006; MOE/NIER, 2008) were developed following the US Environmental Protection Agency and the European Environment Agency (Barbour, 1999; EEA, 1996; US EPA, 2002). The biological survey was conducted twice a year, once during the spring (April–May) and once during the fall (September–October). Species belonging to the three fauna that occupy different locations in the food chain of stream ecosystems (i.e., fish, benthic macroinvertebrates, and epilithic diatoms) were investigated and taxonomically resolved at the species level; for instance, fish were surveyed for all habitat types including riffle, pool, and run, using kick-net (mesh 4 mm) and casting-net (mesh 5 mm); benthic macroinvertebrates were surveyed at riffle habitats using a Surber sampler (30 × 30 cm, mesh 1 mm) (MOE/NIER, 2008). We collected survey data for these three fauna from an 11-year period (2008–2018) from the Water Environment Information System website (<http://water.nier.go.kr/>). The NAEMP targets all streams across the country, with 3 035 survey sites. We used biological survey data from 1 368 survey sites where the Red List species were observed during the 11-year observation period (Fig. 1).

2.2. Food web construction

Food webs consisting of fish–benthic macroinvertebrate–epilithic diatoms were constructed based on the NAEMP biological survey data. The predation links between species were extrapolated based on published species interaction data collected from the Global Biotic Interactions database (Poelen et al., 2014). Constructed food webs with link extrapolation are usually regarded to be high confidence (Gray et al., 2015). However, there could be problems when the interaction data within a database are not well matched with the researcher's own data because the database is incomplete. Considering that the Red List in the regional- or national-level evaluations of threatened species typically includes many endemic species (refer to the Section 2.3) whose distributions are limited, no interaction data that taxonomically exactly correspond at the species level is likely to be within the database. This might methodologically produce hidden links (i.e., links that realistically exist in natural ecosystems but are not realized within constructed food webs) and concomitant isolated nodes, both of which may reduce the confidence of the constructed food webs in this study. Hidden link problems are common in many food web studies, even in food webs constructed based on direct link investigations. For link reliability, we made the additional assumption that taxonomically similar species have taxonomically similar prey or predators, which is supported by the taxonomic similarity of predation characteristics among the species (Eklöf et al., 2012). This was also intended to prevent the Red List species, the main target species in this study, from being lost while building the food web. Consequently, predation links were formed if the data matched at the taxonomic genus level. We automatically generated links and constructed food webs using the R function Webbuilder, developed by Gray et al. (2015). We partly used the family-level matching method for certain species included in the Red List or isolated nodes after the first matching. Additionally, biological survey data tended to be biased towards epilithic diatoms. Too many epilithic diatoms resolved at the species level may lead to a biased web, which may be inappropriate for analyzing species removal effects. Thus, the epilithic diatom species within the survey data were taxonomically lumped into the order level. Finally, 1 368 food webs were constructed and their summary statistics are provided in Table S1.

2.3. The IUCN Red List data and species removal simulation

IUCN developed “Regional Guidelines” for applying the IUCN Red List Criteria for regional or national level assessments (IUCN,

2012). Countries around the world have been building their own Red List in accordance with IUCN's recommendations. The National Institute of Biological Resources in Korea published the first edition of Korean Red Data books, including birds, amphibians, reptiles, fish, mammals, vascular plants, mollusks, and insects for 2011–2014. The publication of the second edition has been in progress since 2019. This study used Red List data for fish, mollusks, and aquatic insects, which are major taxa in stream ecosystems. Following the latest updated information, the Red List for fish was based on the revised edition, whereas the Red List for mollusks and aquatic insects was based on the first edition (NIBR, 2012; NIBR, 2013; NIBR, 2019). This study utilized species data listed in the four categories of the IUCN Red List: CR, EN, VU, and NT (Table 1). The extinction risk is the highest in the following order: CR, EN, VU, and NT.

We performed a species removal simulation based on IUCN Red List categories to test the first hypothesis. It was assumed that sequential cumulative extinction from species with a high extinction risk to species with a low risk of extinction (i.e., from CR to NT) would occur under disturbance. We established three different biodiversity loss scenarios: extinctions of species that belong to 1) CR and EN (low; low degree of biodiversity loss), 2) CR, EN, and VU (medium; medium degree of biodiversity loss), and 3) CR, EN, VU, and NT (high; high degree of biodiversity loss). The extinction of the CR category was not considered an independent scenario because of the small number of species within that category. We performed a species removal simulation for each scenario.

Second, a species removal simulation was performed to determine the effects of extinct taxa. Among the listed species (Table 1), two taxa groups of fish and benthic macroinvertebrates (aquatic insects and mollusks) were separated, and species removal simulations for each taxon group were performed in the original food web. Simulations were performed according to the three biodiversity loss scenarios described above. Additionally, we performed a random species removal simulation to examine the differences in food web impacts between random and realistic species extinctions (more details and results are provided in the Supplementary Material).

Table 1

List of species in the Korean Red List used in this study. Four categories, according to the International Union for Conservation of Nature (IUCN) guidelines, Critically Endangered Species (CR), Endangered Species (EN), Vulnerable Species (VU), and Near Threatened Species (NT), were considered. Data on three stream fauna (i.e., fish, aquatic insects, and mollusks) are shown.

Category	Fish	Aquatic insects	Mollusks
CR	<i>Odontobutis obscura</i> <i>Iksookimia pumila</i> <i>Microphysogobio rapidus</i> <i>Kichulchoia brevifasciata</i>		
EN	<i>Pseudopungtungia nigra</i> <i>Coreoperca kawamebari</i> <i>Pseudobagrus brevicorpus</i> <i>Saurogobio dabryi</i> <i>Microphysogobio koreensis</i> <i>Cobitis choii</i> <i>Koreaocobitis naktongensis</i> <i>Phoxinus phoxinus</i> <i>Acheilognathus somjinensis</i> <i>Liobagrus obesus</i> <i>Gobiobotia naktongensis</i>	<i>Macromia daimoji</i> <i>Libellula angelina</i>	<i>Lamprotula leai</i> <i>Koreanomelania nodifila</i> <i>Corbicula fenouilliana</i> <i>Cipangopaludina japonica</i>
VU	<i>Rhodeus pseudosericeus</i> <i>Pungitius sinensis</i> <i>Gobiobotia brevibarba</i> <i>Hemibarbus mylodon</i> <i>Brachymystax lenok</i> <i>Cottus hangiongensis</i> <i>Ladislavia taczanowskii</i>	<i>Procloeon halla</i> <i>Paracercion sieboldii</i> <i>Boyeria maclachlani</i> <i>Nannophya pygmaea</i> <i>Asiagomphus coreanus</i> <i>Asiagomphus melanopsoides</i>	<i>Sinotaia quadrata</i> <i>Corbicula corolata</i> <i>Clithon retropictus</i> <i>Solemaia triangularis</i> <i>Koreoleptoxis globus ovalis</i> <i>Pisidium coreanum</i> <i>Corbicula papyracea</i> <i>Anodonta arcaeformis flavotincta</i>
NT	<i>Gobiobotia macrocephala</i> <i>Culter brevicauda</i> <i>Pseudopungtungia tenuicorpa</i> <i>Cottus koreanus</i> <i>Acheilognathus signifer</i> <i>Microphysogobio longidorsalis</i> <i>Kichulchoia multifasciata</i> <i>Gasterosteus aculeatus</i> <i>Iksookimia yongdokensis</i> <i>Microphysogobio jeoni</i> <i>Iksookimia pacifica</i> <i>Acheilognathus majusculus</i> <i>Takifugu obscurus</i>	<i>Ephaceraella longicaudata</i> <i>Copera tokyoensis</i> <i>Aeschnophlebia anisoptera</i> <i>Aeshna juncea</i> <i>Lestes temporalis</i> <i>Nihonogomphus minor</i>	<i>Anodonta (Anemina) arcaeformis</i> <i>Laevapex nipponica</i> <i>Corbicula (Corbicula) japonica</i> <i>Corbicula (Corbiculina) ftuminea</i> <i>Semisulcospira tegulata</i> <i>Semisulcospira forticosta</i> <i>Semisulcospira coreana</i> <i>Neosuccinea horticola koreana</i>
Total	35	14	20

2.4. Food web indices and statistical analysis

Six commonly used food web structural indices were used in this study: species richness (S), number of links (L), link density (average number of links per species; LD), connectance (ratio between the number of links realized and the number of links possible; C), generality (mean number of prey per predator; Gen), and vulnerability (mean number of predators per prey; Vul) (Cordone et al., 2020; Ménillet et al., 2022). We analyzed changes in food web indices due to extinction and then tested our hypotheses using a linear mixed effect model (LMM). The LMM for testing the first hypothesis included the differences in food web indices due to extinction (before–after) as a response variable and the biodiversity loss scenario as a fixed effect, and the size of a food web (same as S ; species richness) as a random effect. The LMM for testing the second hypothesis included the extinct taxa group (fish and benthic macro-invertebrates) as a fixed effect, and the rest was the same as the above model. LMMs were fitted using the restricted maximum likelihood method. Details about the random structure selection and evaluation of LMMs and hypothesis testing procedure are provided in Section S1. *Linear mixed effect model and statistical analysis* within [Supplementary Material](#).

3. Results

3.1. Changes in food web structure depending on the degree of biodiversity loss

Changes in food web indices due to extinction differed significantly among the degrees of biodiversity loss, except for connectance (Fig. 2 and Table S3). Significant changes and decreasing trends observed in several food web indices with an increasing degree of biodiversity loss supported our first hypothesis (Fig. 2a, b, c, e, and f). The number of species and generality showed decreasing patterns as the degree of biodiversity loss increased (significant differences among all scenario combinations and decreases in estimated marginal means, $\Delta S = -1.3, -2.1,$ and -4.1 and $\Delta Gen = -0.44, -0.74,$ and -1.24 at low, medium, and high, respectively; Fig. 2a and e, Tables S3 and S4). Two indices, the number of links and link density, exhibited no significant difference between the low and medium scenarios (Fig. 2b and c, and Table S3); however, they showed a significant difference between the two scenarios and the high

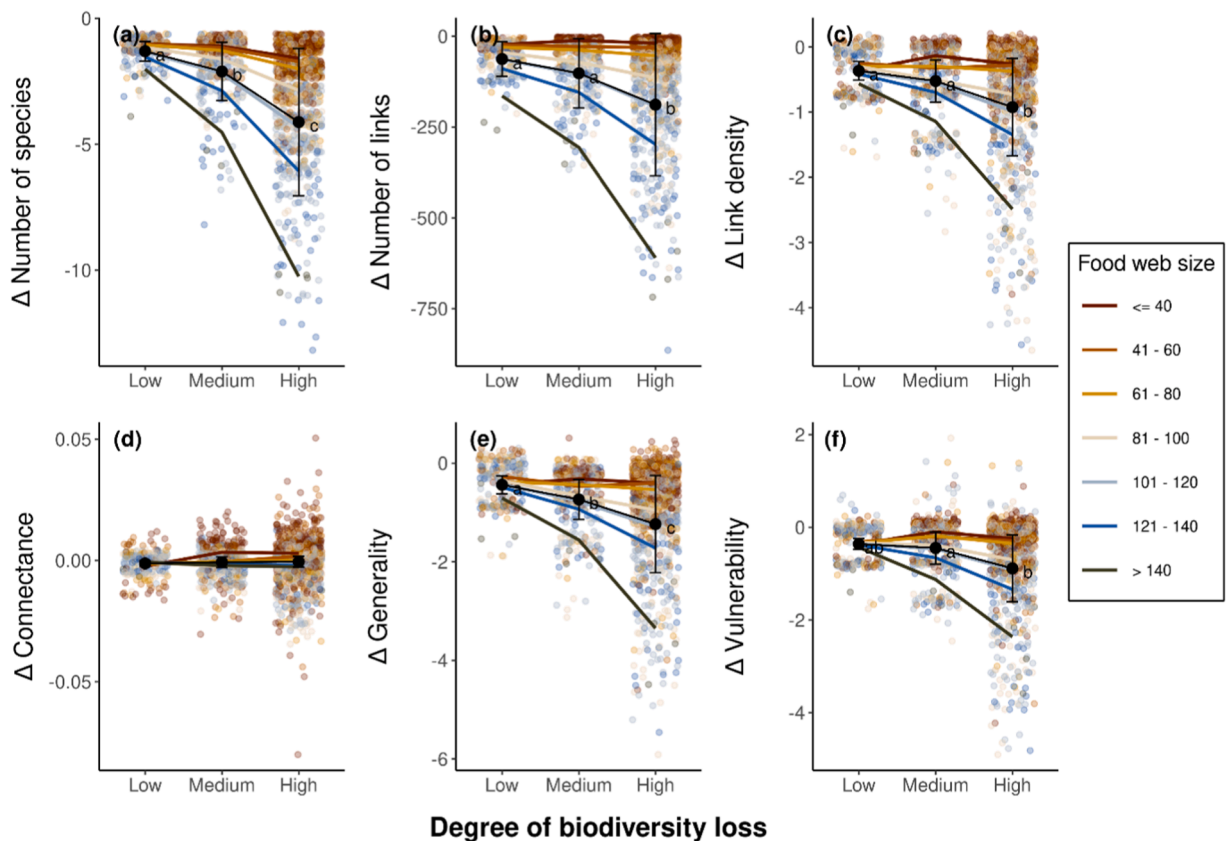


Fig. 2. Changes in food web indices for the different degrees of biodiversity loss (low, medium, and high). Six food web indices, (a) the number of species, (b) the number of links, (c) link density, (d) connectance, (e) generality, and (f) vulnerability, were used. The differences in indices due to extinction were analyzed using a linear mixed effect model. Black dots and lines represent estimated marginal means (color lines represent estimated marginal means per food web size group). Error bars represent 95% confidence intervals from linear mixed effect models. Different letters (a, b, and c) indicate statistically significant differences ($p < 0.05$) among the degrees of biodiversity loss. Jitters indicate data points for each food web.

scenario ($\Delta L = -63, -102, \text{ and } -188$ and $\Delta LD = -0.37, -0.52, \text{ and } -0.92$ at low, medium, and high, respectively; Table S4). Connectance was not affected by the degree of biodiversity loss; however, both positive and negative variations distributed around zero were observed regardless of the degree of biodiversity loss (Fig. 2d). There was a significant difference in vulnerability between the medium and high scenarios (Fig. 2f). Additionally, most of the food web size groups showed a similar pattern with the whole population (i.e., decreasing trends with the increase in the degree of biodiversity loss), except for the two small size groups (≤ 40 and 41–60) showing different trends from other groups (Fig. 2b–f).

3.2. Changes in food web structure depending on the extinct taxa group

Changes in the food web structure due to extinction were significantly different between the two extinct taxa groups ($p < 0.01$ for the number of species and $p < 0.001$ for the other five indices, for slopes of a fixed effect; Fig. 3 and Table S6), supporting our second hypothesis. The results for the number of links, link density, generality, and vulnerability showed that the extinction of the fish group had greater effects than that of the benthic macroinvertebrate group (identified by more negative estimated marginal means and significant slopes; Fig. 3b, c, e, and f and Tables S6 and S7). However, the latter group had a greater effect on the number of species than the former group (Fig. 3a). Interestingly, the two taxa groups showed opposite directions of connectance changes after extinction (negative and positive estimated marginal means for fish and benthic macroinvertebrates, respectively; Fig. 3d and Tables S6 and S7). Additionally, all food web size groups showed the same pattern as the whole population (all negative slopes for the number of species and all positive slopes for the other five indices; Fig. 3).

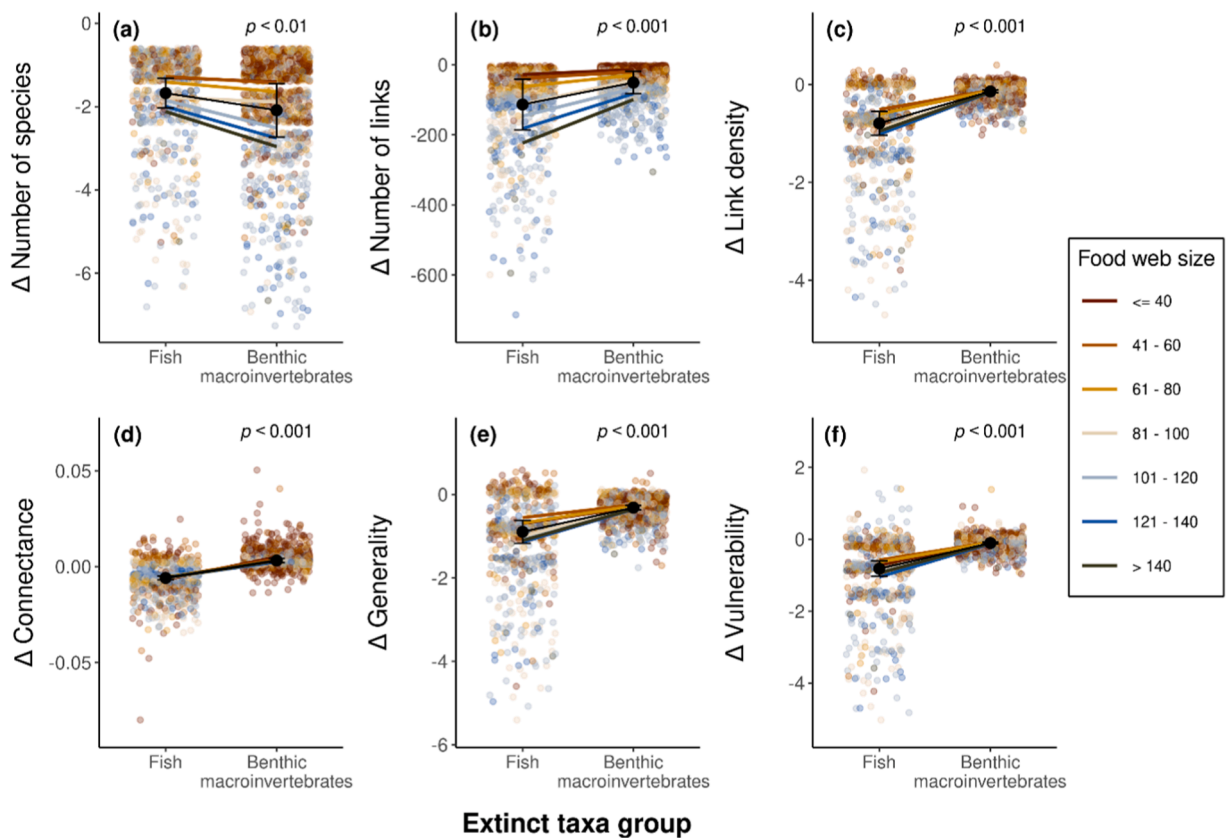


Fig. 3. Changes in food web indices for the extinctions of fish and benthic macroinvertebrates groups. Six food web indices, (a) the number of species, (b) the number of links, (c) link density, (d) connectance, (e) generality, and (f) vulnerability, were used. The differences in indices due to extinction were analyzed using a linear mixed effect model. Black dots and lines represent estimated marginal means (color lines represent estimated marginal means per food web size group). Error bars represent 95% confidence intervals from linear mixed effect models. Significant slopes of a fixed effect indicate statistically significant differences between extinct taxa group effects. The p -value for a slope is presented in the top-right corner of each panel. Jitters indicate data points for each food web.

4. Discussion

4.1. Accumulated extinctions of endangered species may alter the food web structure in stream ecosystems

Notably, our predictions showed significant decreases in most food web indices (S , L , LD , and Gen) with a high degree of loss, including NT species extinction, which was discriminated from the moderate impacts of the two lower-degree losses (Fig. 2). A few studies conducted on other ecosystem types have reported similar results about food web changes (Albouy et al., 2014; Ledger et al., 2013; Márquez-Velásquez et al., 2021). de Visser et al. (2011) showed that, in the Serengeti savanna food webs, the accumulated loss of threatened species would cause the decreases in both L and LD (about -132 and -0.6 , respectively). Hattab et al. (2016) projected food web changes under climate change across the Gulf of Gabes ecosystems in the Mediterranean Sea, showing the decreases in S (-1 to -23), L (-7 to -513), Gen (-0.29 to -6.6), and Vul (-0.51 to -0.89) and both decreases and increases in C (-0.076 to -0.053) in 2080–2099 compared to the present (1982–2009). In the coastal ecosystem study, a decrease in LD has been shown given the assumption of the loss of four species due to overfishing (values were not provided but approximately less than -0.5 from their graphs) (Rocchi et al., 2017). Compared to their results, the magnitudes of the decreases in this study were similar to or more significant than theirs. In particular, the reduction in the two indices, L and LD (-188 and -0.92 at high, respectively; Table S4), which are commonly used indicators of ecosystem complexity and robustness (Dunne et al., 2002), were huger than previous results, suggesting vulnerability of stream ecosystems to disturbances. Decreases in Gen and Vul (-1.23 and -0.88 at high, respectively; Table S4), which present the reductions of diet breadth of consumers and pathways of energy and material, may reduce robustness and enhance extinction probability (Dunne et al., 2002; Hattab et al., 2016). Not all studies conclude that the impacts of species loss will be fatal to ecosystems; however, those studies commonly call for attention to the potential seriousness of food web changes because they subsequently affect ecosystem functions and processes (Ibarra-García et al., 2020; Micheli et al., 2014; Rocchi et al., 2017). What we are stressing here is also in a similar vein to their arguments. Instead of concluding that stream ecosystems are more seriously impacted from species loss than other ecosystems or that the NT level loss necessarily causes critical changes, we suggest that severe biodiversity loss, like the accumulated extinctions of both threatened and near-threatened species, can change food web structure and subsequently impact related fundamental processes such as primary production, decomposition, and respiration (Keyes et al., 2021; Petchey et al., 2004; Thompson et al., 2012). However, these comparisons may be misleading because there exist inconsistencies derived from differences in sampling efforts, taxonomic resolution, aggregation method, and spatio-temporal scales among studies (Martinez et al., 1999; Jordán and Osváth, 2009). Although the webs compared above were of similar size ranges and taxonomic resolutions to ours, discrepancies still remain. Nevertheless, these comparisons can help verify the ecological significance of species loss.

Meanwhile, the impacts of low- and medium-degree biodiversity losses were not significantly different, as shown by several food web indices (e.g., L and LD) (Fig. 2). These results can indicate the robustness of stream ecosystems to weak disturbances, as is known for other ecosystem types, such as terrestrial and marine ecosystems (Burgess et al., 2013; Haddad et al., 2009). The specific structures of ecosystems or dynamic mechanisms, such as highly connected structures, structural and functional redundancy, interaction rewiring, and resource partitioning, make their own systems resilient and stable against disturbances, preventing the collapse or malfunction of ecosystems (Devictor et al., 2008; Lavery et al., 2020). For instance, prey-release in complex food webs can mitigate the impact of biodiversity losses on marine production (Fung et al., 2015). Limited functional redundancy in Indo-Pacific coral reefs could lead to deleterious changes in ecosystem function because of the extinction of only one species (Bellwood et al., 2003). In this study, the high complexity (L , LD , and C) and high generalism of predators (approximately 17 prey species per predator; Gen in Table S1) contributed to the robustness of food webs in stream ecosystems. It has been reported that the high generalism of predators help to prevent trophic cascade effects caused by biodiversity loss because they can switch their prey, dynamically responding to prey loss (Barnum et al., 2015; Rocchi et al., 2017). Although such dynamics were not considered in this study, the robust tendencies observed were also derived from the many alternative prey items of generalists because they can survive even if one or more of their prey items are removed. Therefore, these results imply, in the structural aspect, the importance of generalist predators in conserving stream biodiversity.

Our comparisons between random and realistic species removal simulations further supported the impact of realistic extinctions. For most food web indices, no significant differences were observed between the two sequences; however, greater variation and lower estimated means were observed in the realistic extinction simulations (especially in larger webs; Fig. S1b, c, e, and f). This can indicate that realistic extinction effects may be more severe than random extinction effects. In contrast, Ávila-Thieme et al. (2021) showed that, compared to random extinctions, species losses due to fisheries in the marine ecosystem, which reflect realistic extinctions, had relatively low influences on food web structure. The responses of food webs to realistic extinctions can vary across ecosystem types. Moreover, there are various measures of extinction effects, and the measures used can differ among studies (Ávila-Thieme et al., 2021; Canning et al., 2018; de Visser et al., 2011; Mérillet et al., 2022). Their study used the number of secondary extinctions to compare the impacts of the two extinction sequences; however, these numbers were not directly considered in this study. Nevertheless, some of our simulation results included secondary extinction effects. A few secondary extinctions occurred during random species removal in this study (Fig. S1a). More specifically, the process involved the removal of basal species, which were mostly epilithic diatoms, and their losses caused secondary extinctions of some specialist herbivores unlike the realistic extinction simulations. Notably, realistic extinctions induced a larger number of link losses, even without secondary extinctions, compared with random extinctions. These results suggest that many link losses potentially alter the food web structure, emphasizing the seriousness of the impacts of ongoing biodiversity loss in stream ecosystems (Tylianakis et al., 2010; Valiente-Banuet et al., 2015).

We also observed that the responses to biodiversity loss were considerably different between food webs with different sizes, especially for small food webs (≤ 40). Such size effect of food webs deserves a further study because the size dependency of food web

indices (often called the scale-dependency) is an important issue in ecology (Bersier and Sugihara, 1997; Martinez, 1994). Bersier and Sugihara (1997) reported that small-sized webs could have scale-dependent properties due to their simplistic link structure and subsequent limited range of indices. They presented 12 species as a division point for small size and showed that, even if nodes are aggregated, scale-dependent properties survive but only the division point moves. Considering these properties, small-sized webs have often been excluded from analysis to reduce bias (Sugihara et al., 1989; Ulanowicz, 2009). In this study, diverse sizes were considered and, accordingly, it was expected that indices behavior to species loss would differ between small- and large-sized webs. Our results presented greater changes in large-sized webs with increasing loss degrees while small-sized effects were well controlled (different y-intercepts and slopes by size; Fig. 2). This implies the scale dependency of large-sized webs, which is common in aquatic ecosystems dominated by generalist consumers (Havens, 1992). Because our study used link extrapolation, the predatory links of generalist consumers are expected to be reflected well. In addition, data heterogeneity can cause scale-dependencies of food webs (Bersier and Sugihara, 1997) but that was unlikely to be related to our results because we used uniform taxonomic resolution and node aggregation. Thus, our results suggest that impacts of species loss are different between food webs of different sizes, which requires a further study.

4.2. The loss of fish species more severely impacts stream food webs than that of benthic macroinvertebrate species

We found differences in the net impacts of the extinctions of fish and benthic macroinvertebrate groups, indicating that the extinction of fish groups would cause larger changes in the food web structure, despite their lower extinction numbers compared to the benthic macroinvertebrate group (Fig. 3). This is because fish species tend to be involved in various food web interactions as both predators and prey, as seen in the relatively large declines in *Gen* and *Vul* (Fig. 3e, f). Although the impacts of benthic macroinvertebrate group extinctions were relatively small in this study, their losses could lead to subsequent extinction of the species eating them (Macadam and Stockan, 2015). Benthic macroinvertebrates are the major resources for many predators in stream ecosystems. Moreover, they engage in many important stream functions, dynamics, and ecosystem services, including nutrient cycling, decomposition, and filtration (Macadam and Stockan, 2015; Vaughn, 2018). It has been previously documented that the trophic position of removed species or taxa is a critical factor in determining the outcome of extinction (Donohue et al., 2017; Ebenman et al., 2004). For instance, the removal of top predators in marine systems leads to a reduction in total production through top-down effects (Rupp and Bornatowski, 2021). On the contrary, several studies have revealed that removing basal or intermediate species rather than top predators can cause more secondary extinctions through bottom-up effects (Ebenman et al., 2004; Eklöf et al., 2008). Valuing the relative importance of taxa and setting conservation priorities remains challenging; however, our results highlight the importance of fish groups in sustaining food web structures in stream ecosystems.

4.3. Limitations

There are several caveats when interpreting the results. We have already mentioned the difficulties of food web comparison in discussing the results. Here, we discuss three additional points. First, we used the established biodiversity loss scenarios that rely on the Red lists evaluated based on IUCN protocols; however, there exist numerous non-evaluated species (IUCN, 2022). Furthermore, the scenario settings for different degrees of biodiversity loss remain arbitrary, in spite of the use of IUCN categories with public confidence (Betts et al., 2019). These factors can cause an underestimation of the impact of extinction of endangered species on food webs, which could be far greater than expected. Second, the uses of network indices are useful for comparing food webs; however, if they were not handled carefully, numerical artifacts from the scale-dependencies of network indices can arise (Dunne, 2009). To prevent this, we controlled food web size as a random effect of the model but such size effects may not be completely removed; for instance, two directional changes in $C (L/S^2)$ were observed, which was derived from its dependency of S and L . In addition, there could be a data-derived reason for the different responses between small- and large-sized webs. The webs with ≤ 40 species tended to contain smaller number of endangered species compared to large-sized webs. This could lead to removal of fewer species and subsequently reduce the magnitude of impacts, though this numerical effect was controlled by allowing different variance structures among size groups in the modeling process. In this study, rather than being excluded, these possible scale- or data-driven effects were embedded into the model. This may be more reasonable for accounting for massive web data with complex data structure, which could not be achieved by using simple linear regression models; nevertheless, small sized-webs should be further explored. Despite these scale issues of food webs, many food web studies have contributed to enhancing fundamental understandings of ecosystem changes followed by global changes such as climate change, habitat destruction, and pollution (Keyes et al., 2021; Mellard et al., 2022; Petchey et al., 1999). Our findings can provide an intuitive understanding of the effects of biodiversity loss broadly explicable across different food web sizes. Lastly, this study considered binary food webs due to limited data availability for dynamic food web construction (e.g., weighted webs with biomass flux). Simulations of species removal using binary food webs could be ecologically less feasible than those using quantitative food webs because they cannot take into account secondary extinctions derived from top-down effects and may therefore overestimate food web robustness (Zhao et al., 2016). Thus, cautious interpretation is needed, and dynamic webs also need to be explored as the required data become available.

4.4. Implications for assessment, evaluation, and diagnosis of the ecological impacts of biodiversity loss

Biodiversity conservation focuses on preserving specific biological communities and economically important species (Bachman et al., 2019; Stuart-Smith et al., 2020). Thus, biodiversity has been evaluated based on community-based measurements such as species abundance, richness, and evenness (Bain et al., 2000). The use of these indices provides an intuitive understanding of biodiversity

changes, such as declining species diversity and changes in community structure; however, it cannot demonstrate ecosystem-level properties such as ecosystem responses to exotic disturbances, stability, and resilience. The current field of biological conservation requires predicting and evaluating the ecosystem-level impact of extinction. Recently, a food web framework plays an important role in bridging community structure and ecosystem functioning, and its applications for solving current issues such as climate change and species invasion have rapidly increased (Proulx et al., 2005; Thompson et al., 2012). Many ecologists have suggested that a food web framework is useful in biodiversity conservation, biological monitoring, ecosystem management, and restoration (Keyes et al., 2021; Mellard et al., 2022; Mérillet et al., 2022). In particular, the potential of using food web indices has been continuously emphasized; for instance, Christianen et al. (2017) showed that structural changes in intertidal shellfish reef ecosystems were not detected by community indices, but were revealed by food web indices. This study also demonstrated different changes in the food web and community indices with increasing biodiversity loss. Specifically, several food web indices were less sensitive than the community indices (S in this study), as identified by differences in significant changes among the indices (Fig. 2). Food web indices may provide more conservative evaluations; however, they can be good indicators for detecting significant changes at the ecosystem level. Therefore, we suggest that a food web framework integrated with community-based approaches can be useful for assessing, evaluating, and diagnosing the ecological impacts of biodiversity loss.

Further, we provide three ecological insights into conserving biodiversity from a network perspective. First, preemptive action is highly important in biodiversity conservation. However, the degree of extinction risk of species does not necessarily refer to protection priorities (IUCN, 2001). From the network perspective, our results indicate that the priority species or its range could differ from those previously considered. In particular, we stress the necessity of protecting near-threatened species as well as threatened species, and hence, broader considerations may be needed to prioritize species protection. Second, this study can support the establishment of practical actions to protect biodiversity. Our approach, integrated with the IUCN Red List and food web approaches, can be used to suggest species in need of further protection; for instance, the IUCN category can be used for determining the level of species protection by predicting the magnitudes or fatalness of the impacts of lost species. Lastly, the outcome of extinction depends on the interaction structure of the species being eliminated. Thus, who goes extinct could outweigh how much goes extinct. Although various human compartments, such as social, cultural, economic, and regional factors, should be considered together, there is an urgent need to protect endangered fish. In addition, though we used the Korean stream data, these implications are not restricted to the context of Korea and can be plausible across other countries or regions, as the various web sizes were comprehensively considered while leaving aside other factors.

5. Conclusion

Biodiversity conservation regimes are shifting from conserving individual species to pursuing ecosystem sustainability (Harvey et al., 2017; Tylanakis et al., 2010). This study provides novel insights into the effects of biodiversity loss on stream ecosystems using a simulated food web approach. Our results showed that a high degree of loss of endangered species altered the overall stream food web structure, and the extinction of fish species particularly exerted serious impacts on stream ecosystems. The loss of endangered species and structural changes in food webs may lead to subsequent changes in ecosystem functions and services, which require further investigation. We highlight the importance of protecting and preserving endangered species for biodiversity conservation and suggest that a food web framework can be effectively used in diagnosing ecosystem-level impact of species extinction.

CRedit authorship contribution statement

Minyoung Lee: Conceptualization, Formal analysis, Data curation, Writing - Original Draft, Writing - Reviewing and Editing, Software **Yongseon Kim:** Conceptualization, Resources, Validation **Dougu Nam:** Supervision, Writing - Reviewing and Editing **Kijong Cho:** Supervision, Writing - Reviewing and Editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2023.e02747](https://doi.org/10.1016/j.gecco.2023.e02747).

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