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Uncovering the secrets they keep – the role of parasites in food web ecology

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ABSTRACT

Interactions involving parasites often account for large proportions of links within aquatic food webs, yet few studies integrate parasites into their food web analyses. This analysis compares three sets of highly resolved food webs that differ in taxa composition, space, and time for a subarctic lake system. Key topological food web metrics, including connectance, linkage density, and mean generality and vulnerability, were calculated to explore the impact parasites have on food web structure and functioning. Incorporating parasites into this lacustrine food web was shown to increase connectance, linkage density, and mean vulnerability, a result of unique properties of parasites and the links they participate in. Parasites in the total food web were involved in a large proportion of concomitant predation interactions with their free-living counterparts and numerous trematodes also participated in intra-guild predation, leading to the observed changes in key metrics. Additionally, the division of the total food web into its benthic and pelagic compartments further illustrated that parasites have different impacts in these two highly contrasting habitats, as very different values were reported for most key metrics measured. However, connectance was nearly identical in the two compartments. The higher-than-expected connectance in the benthic compartment was due to the life history strategies of the benthic compartment's parasite taxa. Finally, this analysis explored the impact of a series of fish introductions and the consequences of their ten hitchhiking parasites on the key topological metrics measured. These additional nodes increased linkage density and mean vulnerability but had very little effect on the other measured metrics. This analysis highlights the importance of incorporating parasites, especially trophically-transmitted parasites, into food webs as they significantly alter key topological metrics and are therefore essential for understanding a system's structure and functioning.

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1. INTRODUCTION

Topological food webs map out the trophic relationships occurring within an ecological community (Paine 1980). They are a simplification of who eats who (or what) in a particular ecosystem that includes consumers, producers, and non-living material (Lafferty et al. 2006). Food webs have been used for many decades in ecology to untangle the complicated relationships between predators and prey regulating ecosystem structure, function, and stability (Byers 2009). However, the predator-prey relationship is only part of the story. Parasites are very common consumers in most systems, and yet parasitism is often overlooked in food webs (Marcogliese and Cone 1997, Lafferty et al. 2008). Parasites can have lasting impacts on their host organisms, both at the individual and population levels and on the rest of the ecosystem, leading to profound consequences on community biodiversity and food web complexity (Huxham et al. 1995, Lafferty et al. 2008, Amundsen et al. 2009, Thieltges et al. 2013, Banerji et al. 2015). So why has the incorporation of parasites in food webs only recently and very slowly been adopted by ecologists? Food webs that do not integrate parasites and their links may prevent us from further developing a more accurate food web theory and may lead to erroneous conclusions concerning how ecosystems are structured and how they function. Only by integrating parasites into food webs can we really understand how ecosystem manipulations, such as species invasions and extinctions, affect a system (Lafferty and Kuris 2009, Britton 2013, Llopis-Belenguer et al. 2020, Llaberia-Robledillo et al. 2022). In these scenarios, introduced species may also create new parasite-host links if the invader introduces hitchhiking parasites or if the invader itself acts as a new host for a native parasite species (Amundsen et al. 2013, Britton 2013, Kuhn et al. 2015, Lagrue 2017). The present study examines the impacts of such integration of parasitic species and their corresponding links on the food web topology of a subarctic lake ecosystem including a comparison of the benthic and pelagic food web compartments, while simultaneously investigating the effect of the previous introductions of two fish species and their hitchhiking parasites to the system.

Historically, food webs have rarely included parasites. A principal reason for this seems to be the difficulty in sampling parasites due their inconspicuous size (Lafferty et al. 2006). However, there are numerous reasons to include parasitic interactions in a food web. To start with, parasites are omnipresent and occur commonly in most systems (Carlson et al. 2020). When a parasite establishes in or on a host individual, that parasite commandeers the host's

energy for its own development. This exploitative behavior has many negative consequences for the host, including increased energy expenditure and decreased growth rates (Lafferty and Shaw 2013). Additionally, some parasites can alter an infected host's behavior or morphology to increase the host's vulnerability to predation from free-living taxa (Poulin and Thomas 1999, Miura et al. 2006). Furthermore, parasites should be considered in food web analyses because the energy costs and increased vulnerability incurred by infected hosts can augment network stability (Dobson et al. 2006, Amundsen et al. 2009). Trophic niche specialization and competitive release (or perhaps relaxation) driven by parasite infections may enable similar species to coexist in a system (Hatcher et al. 2006, Britton and Andreou 2016, Rovenolt and Tate 2022). While the inclusion of parasites in food web analyses is a relatively new approach in community ecology studies, it is commonly agreed upon that parasites' wide diversity and unique functional roles alter our understanding of an ecosystem's structure and functioning. Parasites in particular have been found to alter network structure and common food web metrics, such as the number of links and trophic levels, food chain length, connectedness, and nestedness - factors that all are considered important for food-web complexity and stability (Hernandez and Sukhdeo 2008, Lafferty et al. 2008, Amundsen et al. 2009, Thieltges et al. 2013, Morton and Lafferty 2022).

Including parasites in food web modeling can also be important for discerning how species introductions may affect the structure and functioning of the ecosystem. Parasites can successfully establish in a new system by tagging along as hitchhikers when their free-living host is being introduced (Amundsen et al. 2013, Kuhn et al. 2015). Once established in a new system, the parasite may also be able to infect a native species via "host-switching" through a process known as spillover (Britton 2013, Lagrue 2017, Chalkowski et al. 2018). The parasite may host-switch to a native species similar to the introduced host or it may infect a native species in which it can complete other life cycle stages (Britton 2013, Lagrue 2017, Chalkowski et al. 2018). The introduced free-living species may also acquire novel parasites in the new system by consuming infected prey. Invading species are especially vulnerable to such infections as they often lack evolutionarily derived defenses against parasites found in the novel system (Lagrue 2017, Chalkowski et al. 2018, Llaberia-Robledillo et al. 2022). Furthermore, native parasite acquisition in invading species may also lead to spillback of native parasites, in which an introduced free-living species infected with a native parasite is consumed by a native free-living species and thereby infecting the native free-living species with a native parasite it had not been previously vulnerable to. (Lagrue 2017, Chalkowski et

al. 2018, Llopis-Belenguer et al. 2020). All these scenarios would likely increase the connectedness of a system by introducing new links and potentially further increasing the parasite's dispersal ability, even sometimes between different trophic levels. Therefore, parasites should be considered when analyzing the impact of species introductions on food web topology.

Freshwater systems have long been used as model systems for food web analyses (Forbes 1887, Lindeman 1942, Carpenter et al. 1985, Havens 1992, Cohen et al. 2003, Hernandez and Sukhdeo 2008, Preston et al. 2014) and have also been the subject of numerous parasitological studies (Marcogliese 2001, Kennedy 2009, Thieltges et al. 2013, Sures et al. 2017, Giari et al. 2020, Shaw et al. 2020). However, despite these efforts to study food webs and parasites of freshwater systems, there are still major gaps in our knowledge on the role of parasites in the food web topology of freshwater ecosystems. Worldwide, there are few freshwater systems that have been subject to studies considering how parasites may impact food web ecology (Anderson and Sukhdeo 2011). Quick Pond in California, USA is the only lentic system to date in which the ramifications of integrating parasites into the full food web have been examined comprehensively (Preston et al. 2014), concluding that parasites increased most food web topology metrics, including linkage density and connectance. Additionally, very little is known about how parasites contribute to the distinct characteristics and functioning of the pelagic and benthic compartments of a lacustrine system. These two contrasting habitats within a lake are likely to host different parasite communities that reflect each habitat's physical properties, the life history strategies of the compartments' free-living communities, and the function of each compartment in the whole lake ecosystem (Campbell et al. 1980, Marcogliese 2002). The open water characteristic of the pelagic habitat hosts a very particular and adapted set of free-living taxa. Meanwhile, the benthic habitat is populated by taxa exploiting more physically complex structures of the lakebed. Isolating these two habitats into their own compartments in the total food web allows for a more comprehensive investigation into the role of parasites in altering network metrics and the functioning of a food web. Finally, while several studies have examined how such hitch-hiking parasites may alter trophic relationships and food web structure (Torchin et al. 2005, Lafferty and Kuris 2009, Lima Jr et al. 2012, Amundsen et al. 2013), no previous studies have attempted to model the impact of introduced free-living species as well as their co-introduced parasites in the context of the total lentic food web.

The present study addresses the food web and parasites of Takvatn, a subarctic lake in Norway that has been subject to numerous ecological and parasitological studies since the 1980's (Amundsen 1989, Amundsen et al. 1993, Persson et al. 2007, Amundsen et al. 2009, Amundsen et al. 2013, Kuhn et al. 2015, Henriksen et al. 2016, Henriksen et al. 2019a, Henriksen et al. 2019b). Two pilot studies considering the impact of parasites on the food web have recently been conducted in the lake (Amundsen et al. 2009, Amundsen et al. 2013). These studies were confined to the pelagic compartment of the food web. The first addressed how the inclusion of parasites affected common measurements of food web structure and complexity (Amundsen et al. 2009), and the second examined the consequences of the introduction of two non-native fish species on the food web topology (Amundsen et al. 2013). In the recent decade following the pilot studies on Takvatn's pelagic compartment, additional extensive studies have been conducted on the benthic compartment. This has allowed for the current examination of Takvatn's total food web. While such an approach introduces complexities to data collection and modeling, it is a step towards reaching a more realistic analysis of the whole system. Without accounting for parasites in a system's total food web, we cannot assume to make definitive conclusions concerning that specific system or others like it. This becomes especially problematic when attempting to make predictions about how future species introductions, diseases, and even climate change may impact our ecosystems. In this respect, Takvatn's history of species introductions and established theme of trophic ecology and parasitology research makes it an excellent model system for such a comprehensive analysis.

This study has three primary aims. The first is to explore the impact parasites may have on food web topology and common network metrics, and ultimately, system stability by contrasting Takvatn's food web with and without parasites (i.e., the total web including parasites versus the free-living, predator-prey web). I hypothesize that the inclusion of parasites will increase key metrics such as connectance and linkage density. The second aim is to explore and contrast the topological role of parasites in the pelagic and benthic compartments and how they shape the structure and functioning of these compartments. Parasites are hypothesized to have different network impacts on the trophic assemblages of these two highly contrasting habitats. The final aim is to analyze how food web topology may be affected by species introductions and to what extent parasites play a role in these changes. This will be accomplished by comparing Takvatn's total food web before and after the introduction of two fish species by contrasting a reconstructed, pre-introduction trophic web

with the current food web of the lake. The two introduced fish species are hypothesized to prove important for the topology of Takvatn's food web and alter the topological metrics measured, especially through the impact of possible hitchhiking parasites that were co-introduced to the system. Overall, we know parasites are key species for ecosystem functioning and tightly woven within food webs. Therefore, it is vital to discern the impact parasites may have on trophic interactions and ecosystem structure, functioning, and stability within a freshwater system.

2. METHODS

2.1. Study System

The Norwegian lake Takvatn (-vatn or vannet is the Norwegian word for lake) is located 300 km north of the Arctic Circle in the County of Troms at 69°07' N, 19°0 E. The lake itself is situated 214 m above sea level and has an area of 15 km². Takvatn contains two main basins, each measuring over 80 m in depth (88 m at its deepest point). From November to late January Takvatn experiences 24 hours of darkness and from late May to late July, 24 hours of daylight. The lake is typically ice-covered from November or December to May or June. The average air temperature is -10 °C in January and 13.2 °C in July. The maximum epilimnetic water temperature is c. 14 °C. Takvatn is a dimictic and oligotrophic lake with the total phosphate concentration never exceeding 5µg/L, while the Secchi depth typically measures between 14 and 17 m (Primicerio and Klemetsen 1999). Surrounding Takvatn is a landscape of mountains, birch-dominant forest scattered with pine trees, and patches of farmland.

Historically, brown trout (*Salmo trutta*) was the only fish present in Takvatn. However, over-fishing with gillnets in the early 1900's eventually led to low catches. In 1930, arctic charr (*Salvelinus alpinus*) was deliberately introduced from Lake Fjellfrøsvatn, located just 6 km from Takvatn (Klemetsen et al. 1989). The introduced arctic charr (hereafter referred to as charr) population rapidly increased, ultimately leading to food limitations and stunted growth of the dense charr population in Takvatn (Amundsen and Klemetsen 1988, Amundsen 1989). In an attempt to release both the stunted charr and the waning brown trout (hereafter referred to as trout) populations from food limitations and depleted growth rates, three-spined stickleback (*Gasterosteus aculeatus*) was deliberately introduced in 1950 from Lake Sagelvvatn, located 5 km from Takvatn in a different watercourse (Klemetsen et al. 1989, Kuhn et al. 2015).

Takvatn's fish populations have been sampled annually since 1980, with other taxa increasingly sampled throughout the decades. The analysis that came from this sampling and Takvatn's history of fish stocking and stunted charr population inspired the initiation of a management program in the lake. Between the years 1984 and 1991, an intensive fishing program was carried out by local landowners, local fishing association members, and researchers from the University in Tromsø. Over the eight years of fishing the program

removed about 700,000 charr individuals, the equivalent of approximately 35 metric tons or about 80% of the charr population (Amundsen et al. 2019).

2.2. Data Collection and Food Web Matrix Construction

The current food web analysis is based on an $n \times n$ matrix consisting of n species in which the columns represent consumers (predators and parasites) and the rows represent resources (prey and hosts) (Cohen 1978, Lafferty et al. 2006). The study focuses on the topological food web in which all the trophic interactions included in the addressed network arise from detritus, phytoplankton, and aquatic plants as the basal energy sources. Both free-living species and trophically and non-trophically transmitted parasites are included in the food web. Free-living taxa are understood to be non-parasitic organisms involved in classic predator-prey interactions within a food web. Numerical code entries indicate the type of trophic interaction between two taxa. The food web is spatially restricted to the lacustrine habitat, however, terrestrial input to the lake and terrestrial predators that rely on the lake's production are also included (i.e., the bird taxa and the sole mammalian species – the mink). This includes the input of terrestrial organic matter and terrestrial surface insects, which come directly from the terrestrial system and do not feed on anything in the freshwater system but are an important aspect of the trout and charr diet in the fall (Milardi et al. 2016, Prati et al. 2021). Furthermore, the food web is temporally restricted to include taxa and interactions occurring during the ice-free season of Takvatn.

The preferred unit resolution of nodes in this analysis is the species level. Most producers, consumers, and parasites were identified to the species or genus level. However, several groups of algae (periphyton and phytoplankton), bryophytes, terrestrial vegetation, terrestrial surface insects, Nematoda, Ostracoda, and Hydracarina are not resolved to the species or genus level because these groups have been less intensely studied or have a complex taxonomy. Similarly, most microorganisms are not included in the matrix, however, the most common algae as well as rotifers and parasitic fungi were included due to their presumed importance. The species list is based on data from 40 years of annual sampling conducted at Takvatn and constructed using various sampling methods targeting specific taxa in both the pelagic and benthic compartments (Amundsen and Klemetsen 1988, Amundsen 1989, Dahl-Hansen 1995, Knudsen et al. 2001, Klemetsen et al. 2002, Amundsen et al. 2007, Amundsen et al. 2009, Amundsen et al. 2013, Kuhn et al. 2015, Frainer et al. 2016, Henriksen et al. 2016, Soldánová et al. 2017, Amundsen et al. 2019, Henriksen et al. 2019a, Henriksen et al.

2019b, Klemetsen et al. 2020, Prati et al. 2020a, Prati et al. 2020b, Shaw et al. 2020, Prati et al. 2021). In the pelagic, phytoplankton were sampled using Ruttner samplers and rotifers were sampled with Schindler-Patalas traps, which were also used to sample zooplankton in addition to net hauls (Primicerio and Klemetsen 1999, Primicerio 2000). Littoral benthos were collected using Ekman grab, colonization traps, vacuum pumps, sled net samplers, and kick-nets (Klemetsen and Elliott 2010, Frainer et al. 2016, Klemetsen et al. 2020). Profundal benthos were sampled using Ekman grab. Fish sampling was conducted using multi-mesh gillnets in the littoral, pelagic, and profundal zones of the lake (Klemetsen et al. 2002, Amundsen et al. 2019). Birds present at the lake were recorded from observational surveys (Klemetsen and Knudsen 2013). For each sampling method, only free-living taxa that comprised over 1% of the total number of individuals sampled in each sampling year were included in the species list. However, there were a few taxa that failed the abundance criteria and yet were still included in the species list due to their importance as food resources (several cladocerans and chironomids), hosts for parasites (two coleopterans, an ephemeropteran, and a plecopteran), or high-level predators (mink, and several bird taxa).

Extensive parasite sampling in the fish populations has been carried out on an annual basis since 1980 with occasional observations of parasites present in other organisms (Knudsen et al. 2001, Klemetsen and Knudsen 2013, Thieltges et al. 2013, Kuhn et al. 2016, Henriksen et al. 2019a, Prati et al. 2020a). Since 2012, more extensive parasite analyses of invertebrates have been implemented in which arthropods and annelids have been squeezed between glass plates to release and identify parasites, and mollusks have been crushed and their tissue removed for further inspection (Soldánová et al. 2017, Shaw et al. 2020). All species identified in the parasite screenings were included in the Takvatn web. A comprehensive literature review was also conducted to identify potential parasites of the free-living species present in the system.

The main trophic relationships included in this analysis were predator-prey, predator-parasite, parasite-host, and parasite-parasite. These four main categories of interactions are further split into thirteen more specific link types (**Table 1**). Most feeding links for fish were identified via stomach content analysis data from the past 40 years of research at Takvatn (Amundsen 1989, Knudsen et al. 2001, Klemetsen et al. 2002, Amundsen et al. 2007, Kuhn et al. 2015, Henriksen et al. 2016, Soldánová et al. 2017, Henriksen et al. 2019a, Henriksen et al. 2019b, Prati et al. 2020a, Prati et al. 2020b, Shaw et al. 2020, Prati et al. 2021). However, most

predator-prey trophic interactions were based on literature. Yet, prey information in these published studies is provided at a higher taxonomic level than the resolution of the nodes used in this food web. In these cases, links with taxa in these wide groups were included only if the prey taxon was of “suitable” prey size and its habitat overlapped that of the predator.

Similarly, predator-parasite links representing free-living predators consuming free-living

Table 1. Summary of the four link categories (consumer-resource) and the 13 link types observed in the Takvatn food web.

Link Category (Consumer-Resource)	Link Type	Link Description
Predator-Prey	Predation	Consumer kills and feeds on more than one individual of the prey (resource) species.
	Detritivory	Consumer feeds on or breaks down dead and decaying animal and plant matter.
	Cannibalism	Special case of predation in which the consumer and resource are the same species.
Predator-Parasite	Predation on Free-Living, Non-Feeding Stages	Consumer feeds on free-living parasite, but the parasite is not able to infect the consumer and is digested.
	Concurrent Predation on Symbionts	Consumer feeds on parasite living inside a prey, but the parasite is not able to infect the consumer and is digested.
	Trophic Transmission	Consumer feeds on parasite living inside a prey, and the parasite is able to infect the consumer.
	Infection by Predation on Free-Living, Non-Feeding Stages	Consumer feeds on free-living parasite, and the parasite is able to infect the consumer.
Parasite-Host	Macroparasitism	Consumer (parasite) infects a host but does not necessarily cause the death of its host. The consumer (parasite) is not trophically transmittable to other hosts.
	Trophically-Transmitted Parasitism	Consumer (parasite) infects a host but does not cause the death of its host. The consumer (parasite) requires its host to be consumed by an appropriate predator host to complete its life cycle.
	Pathogen Infection	Consumer (parasite) infects a single host and multiplies within that host, often resulting in the death of the host.
	Parasitic Castration	Consumer (parasite) blocks the reproduction of the host.
	Trophically-Transmitted Parasitic Castration	Consumer (parasite) blocks the reproduction of the host and requires its host to be consumed by an appropriate predator host to complete its life cycle.
Parasite-Parasite	Parasite Intraguild Trophic Interaction	Infection agent (parasite) attacks and kills (and often consumes) another infectious agent (parasite) within the same host.

stages of parasites were also inferred from the literature and were based on “suitable” prey size and habitat overlap between taxa. Trophically transmitted parasites can also be used as indicators of their hosts’ diet, as living parasites are able to remain in the host much longer than food items are digested through the gut (Huxham et al. 1995, Marcogliese 2004). Therefore, some predator-parasite links between free-living predators and trophically transmitted parasites were included in the web via direct observation when the parasite was found in the consumer. Most of the included parasite-host links were based on direct observations from Takvatn, however some were inferred from the literature. In some cases, known parasitic life cycles aided in connecting parasites to hosts that were not dissected, for example the trematodes and their final bird hosts (which have not been possible to sample at Takvatn). All parasite-parasite links consist of trematodes feeding on each other and were inferred from the published literature. Links were also inferred for some understudied species based on diet observations from other lakes with the same or analogous species to those present in Takvatn. Such links could also be inferred via known parasite life cycles that are known to infect similar hosts elsewhere. For each consumer, while rare prey taxa were included in the links list, accidental prey were not.

To accomplish the comparisons outlined in the aims above, five web versions were created. They are detailed below.

2.2.1. Total Web vs. Free-Living Web

Takvatn’s total food web was developed first. Takvatn’s total web includes all predators, prey, parasites, and host taxa. Accordingly, this web considers all predator-prey, parasite-host, predator-parasite, and parasite-parasite interactions. Parasite-host interactions include only those in which a parasite is infecting its host. Predator-parasite interactions illustrate links when a predator consumes a parasite. This includes predation on free-living, non-feeding parasites, such as fungi, cestodes, and trematodes. It also includes concomitant predation upon parasites in which an infected prey item is eaten by a predator, but the parasite is not able to establish in the predator and so is merely digested and dies (Thieltges et al. 2013). Not only does this occur when a predator species is not a suitable host for the parasite species, but also when a parasite simply does not infect a suitable host species, as it is estimated that in some parasite-host relationships only 10% of ingested parasites infect their suitable host (Lafferty 1999). The final type of interaction is comprised of trophic relationships between parasites. This intraguild

predation is prevalent among larval trematodes when they share a common host individual (typically snails) and furthermore share an infected organ (Kuris 1990, Lafferty et al. 1994). Following the creation of the total food web, Takvatn's free-living web, consisting of the classic predator-prey trophic interactions between free-living taxa, was developed. This web corresponds to most published food webs and does not include any parasites. The free-living web was constructed by removing all parasite taxa and their corresponding links from the total Takvatn food web. In this respect, it should also be mentioned that the Takvatn food web includes one node (representing water mites) that consists of a parasitic life stage and a free-living life stage and is, therefore, recognized as both parasitic and free-living. The free-living web only incorporates the free-living life stage and the predator-prey interactions linked to that life stage.

2.2.2. Benthic Compartment vs. Pelagic Compartment

For further comparison, Takvatn's total food web was split into the pelagic and the benthic compartment. Each free-living node was assigned to one of these main compartments based on their predominant habitat use. However, seven nodes, including the three fish species, three duck taxa (*Melanitta nigra*, *Melanitta fusca*, and *Bucephala clangula*), and a cladoceran (*Polyphemus pediculus*), can be found in both the pelagic and benthic habitats of Takvatn, and so were represented in the analysis for both compartments. Parasites were assigned to a compartment based on the compartment that their hosts are typically found in. All trematodes were assigned to the benthic compartment, as this is where their key hosts are infected, including their obligatory first host – mollusks. The pelagic compartment contained only taxa assigned to the pelagic and only links among those taxa, and likewise with the benthic compartment, including the seven taxa assigned to both. Furthermore, for the purpose of the intended analysis and comparison, all links between the two compartments were removed to ensure isolation between the pelagic and benthic compartments.

2.2.3. Post-Introduction Web vs Pre-Introduction Web

Takvatn's post-introduction web is the same as the total web described above, whereas for the pre-introduction web, the total food web was heuristically reconstructed to represent the trophic interactions present in the system prior to the introduction of the two fish species. For this retrospective reconstruction of the pre-introduction web, charr and three-spined stickleback (hereafter referred to as stickleback) were removed, along with

their associated links. Subsequently, parasite taxa relying on charr and/or stickleback to complete their life cycle were removed. Finally, free-living consumers with no other prey species in the system were also removed. These taxa would have relied on the introduced species as obligate nutritional resources, and therefore would not have been able to exist in Takvatn prior to the fish introductions. Manipulating food webs by adding or removing species and links in this way can be a useful tool for understanding how species introductions alter the system by establishing new predator-prey and/or parasite-host links (Amundsen et al. 2013). However, this reconstructed food web does not consider species extinctions caused by the fish introductions as there is no data to support or disprove such conclusions. While extinctions are plausible and could potentially alter the results of this study, the reconstruction approach used for this analysis can only examine how the two introduced fish aided in the colonization of new taxa in the system.

Notably, the only mammal present in the system, American mink (*Neovison vison*), is an invasive species known to have escaped from mink farms. However, the first American mink (hereafter referred to as mink) farm in Norway was established in 1927 and escaped mink likely did not establish permanent populations until 1993 (Bevanger and Henriksen 1995). Accordingly, it was reasonable to also remove the mink from the pre-introduction web, as it is very unlikely that any mink were present in the system prior to the first fish species introduction in 1930.

2.3. Network Analyses

To decipher the complicated relationships among all free-living and parasitic taxa regulating ecosystem structure, function, and stability, I calculated and compared eight key food web metrics for the food webs (**Table 2**). Besides the number of nodes and observed links, I also calculated connectance, linkage density, number of trophic levels, mean degree, mean generality, and mean vulnerability. The potential number of links is calculated by a power relationship (n^2) totaling all the cells in a symmetrical $n \times n$ matrix. The proportion of all possible links that are in fact observed in the food web is called connectance. Connectance is closely related to linkage density, which is a measure of the ratio of the observed number of links to the number of nodes. The number of trophic levels was also calculated for each food web. To better understand diet breadth and vulnerability, the average number of links in which a species is consuming or parasitizing another species and the average number of links in which a species is consumed by or parasitized by another species were measured as mean

generality and mean vulnerability, respectively. While mean vulnerability was calculated using all links, calculations for mean generality did not include concomitant predation. This link type does not contribute energetic value to the predator, nor does it impact the web's flow of energy (Morton and Lafferty 2022). All calculations for this analysis were completed in RStudio Version 1.1.463 with the packages “igraph” and “NetIndices”.

Table 2. Summary of the eight key topological metrics measured in all three food web comparisons of Takvatn.

Metrics	Definition
Nodes	Species richness; S
Observed links	L
Potential links	$L_p = S^2$
Trophic levels	$TL_{\text{predator}} = 1 + \sum(TL_{\text{prey}} * 1/\# \text{ of prey})$
Linkage density	$D = L/S$
Connectance	$C = L/L_p$
Mean Generality	Average # of prey taxa
Mean Vulnerability	Average # of predator taxa

3. RESULTS

3.1. Total Web vs. Free-Living Web

The total food web including parasite-host relationships consisted of 174 nodes dispersed across four trophic levels and comprised of 35 basal species, 95 free-living consumers, and 45 parasitic taxa (**Figure 1, Table 3**). Note that one node, the water mites (Hydracarina), has both a parasitic and a free-living life stage, thus acting both as a parasite and a free-living predator in the web. In contrast, the free-living web was made up of 128 nodes spread across four trophic levels. This web contained only 33 basal species and 95 free-living consumers. In this web, the water mites were only represented by their free-living node and its corresponding links. The difference in the number of basal species relative to the total web is due to two inedible phytoplankton species (*Planktothrix mougeotii* and *Tabellaria flocculosa v. geniculata*), whose only connection to the rest of the web is that they are parasitized by chytrid fungi and thus were not included in the predator-prey web. With the addition of 45 parasites in the total web, the number of links more than doubled from 2017 to 4314, which increased linkage density from 15.76 in the free-living web to 24.79 in the total web (**Table 3**). Accordingly, while parasites only accounted for 26% of all nodes, parasitic links made up

Table 3. Summary of calculated key topological food web metrics for the total web and the free-living web.

Metrics	Total Web (with parasites)	Free-Living Web
Nodes	174	128
Observed Links	4314	2017
Connectance	0.142	0.123
Linkage Density	24.79	15.76
Max Trophic Level	4.8	4.0
Mean Degree	49.59	31.52
SD Degree	30.83	19.03
Mean Generality	13.63	15.76
SD Generality	16.69	18.46
Mean Vulnerability	24.79	15.76
SD Vulnerability	19.12	10.82

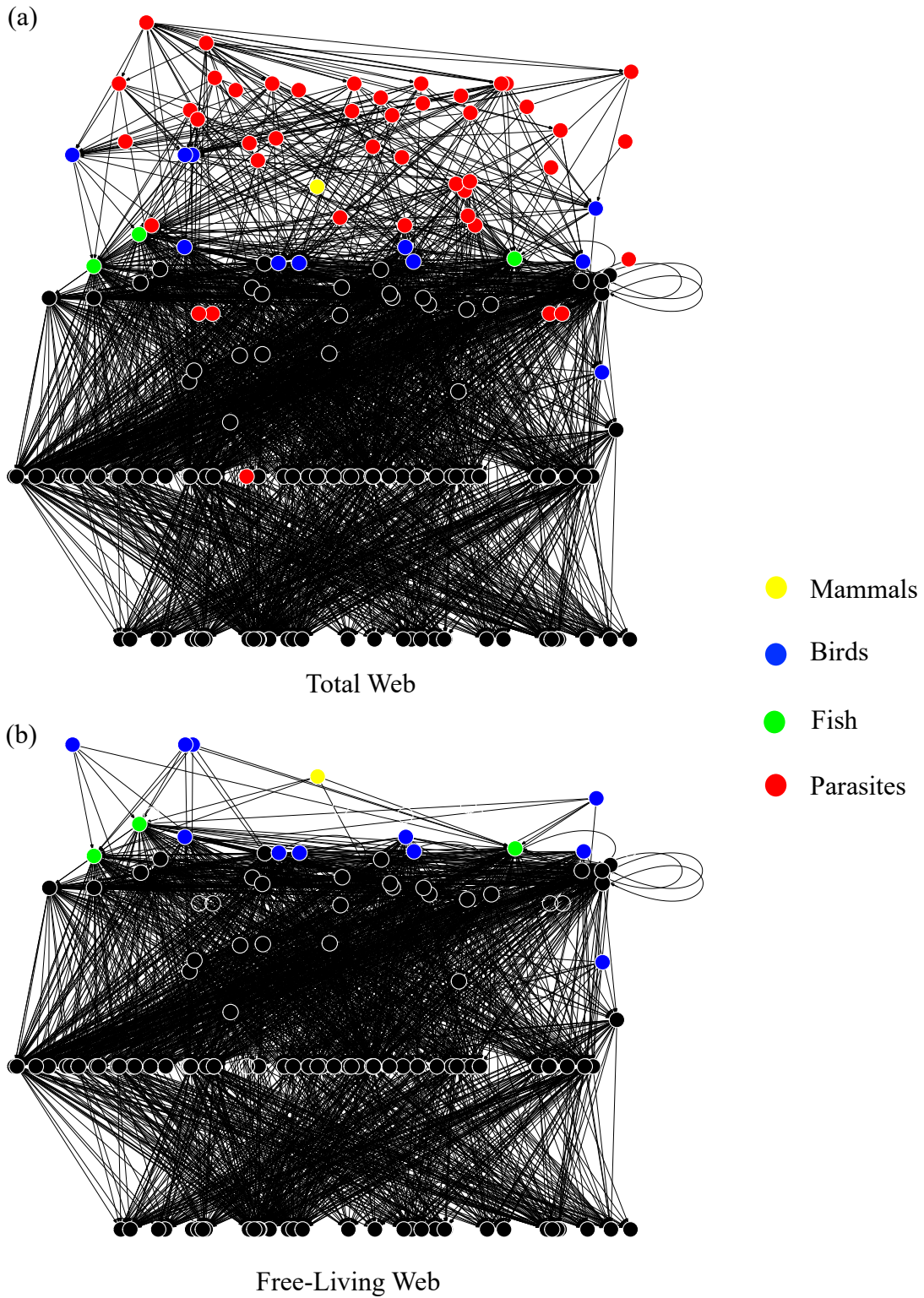


Figure 1. Food web of Takvatn (a) with and (b) without parasites and their related links. The single mammal (*N. vison*) is depicted in yellow. The 11 bird taxa are depicted in blue. The three fish species are depicted in green. The parasites are depicted in red.

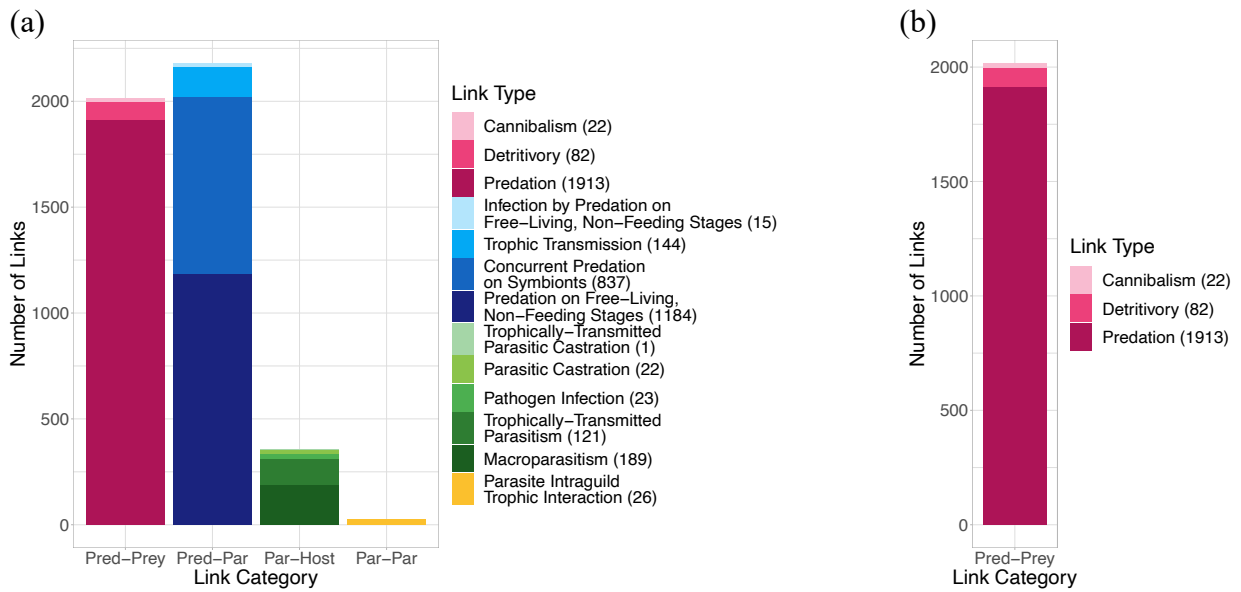


Figure 2. The number of links in (a) the total web and (b) the free-living web. Each of the four link categories are subdivided into its corresponding link types. The number of links observed in each link type is presented in parentheses next to the link type name in the legend. The free-living web only contained one link category, so only that link category is presented.

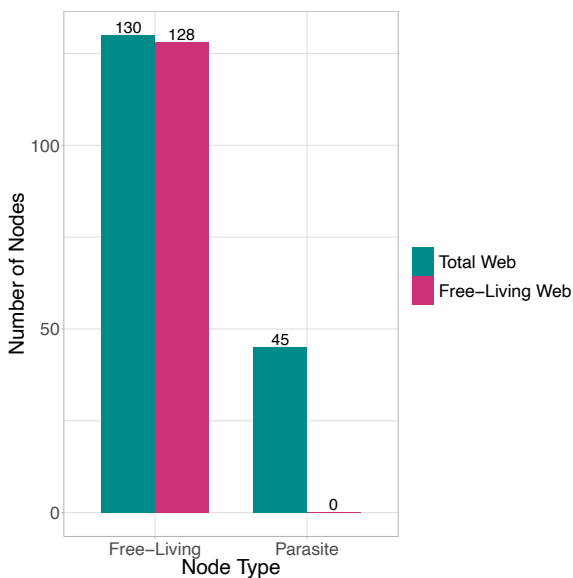


Figure 3. The total number of nodes in each web divided into free-living nodes and parasitic nodes.

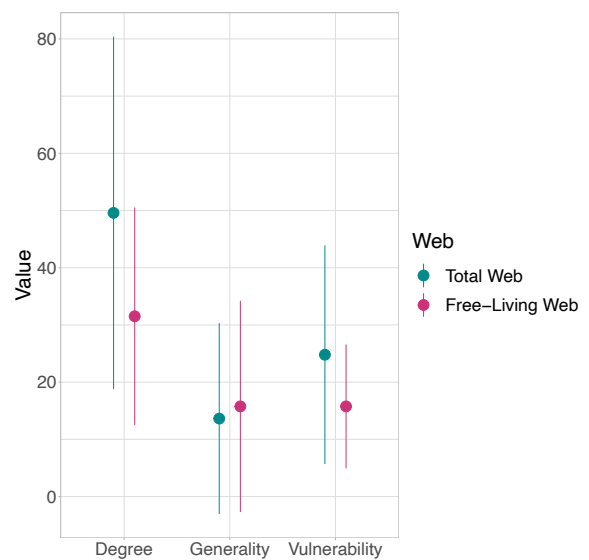


Figure 4. Mean degree, generality, and vulnerability and their respective standard deviations in the total web and free-living web.

53% of all trophic interactions in the total web (**Figure 2, Figure 3**). Additionally, the inclusion of parasites ultimately led to an increase in connectance from 0.123 to 0.142. Mean generality and vulnerability also changed with the inclusion of parasites. In the free-living web, each predator consumed an average of 15.76 prey taxa, while in the total web, each node on average only consumed or parasitized 13.63 taxa (**Figure 4**). The lower mean generality observed in the total web is caused by a lower average parasite mean generality – calculated at only 8.46 – with most parasites infecting or consuming fewer than ten taxa (**Figure 5a**). This trend was reversed for mean vulnerability, where the average number of enemies per node in the total web was much higher than in the free-living web (24.79 vs 15.76) due to a high parasite vulnerability (mean 43.73), as well as a higher free-living vulnerability (mean 18.18) in the total web. While most free-living taxa were vulnerable to 10 to 30 taxa, parasites had either few enemies or many enemies, with few taxa having between 40 and 70 enemies (**Figure 5b**).

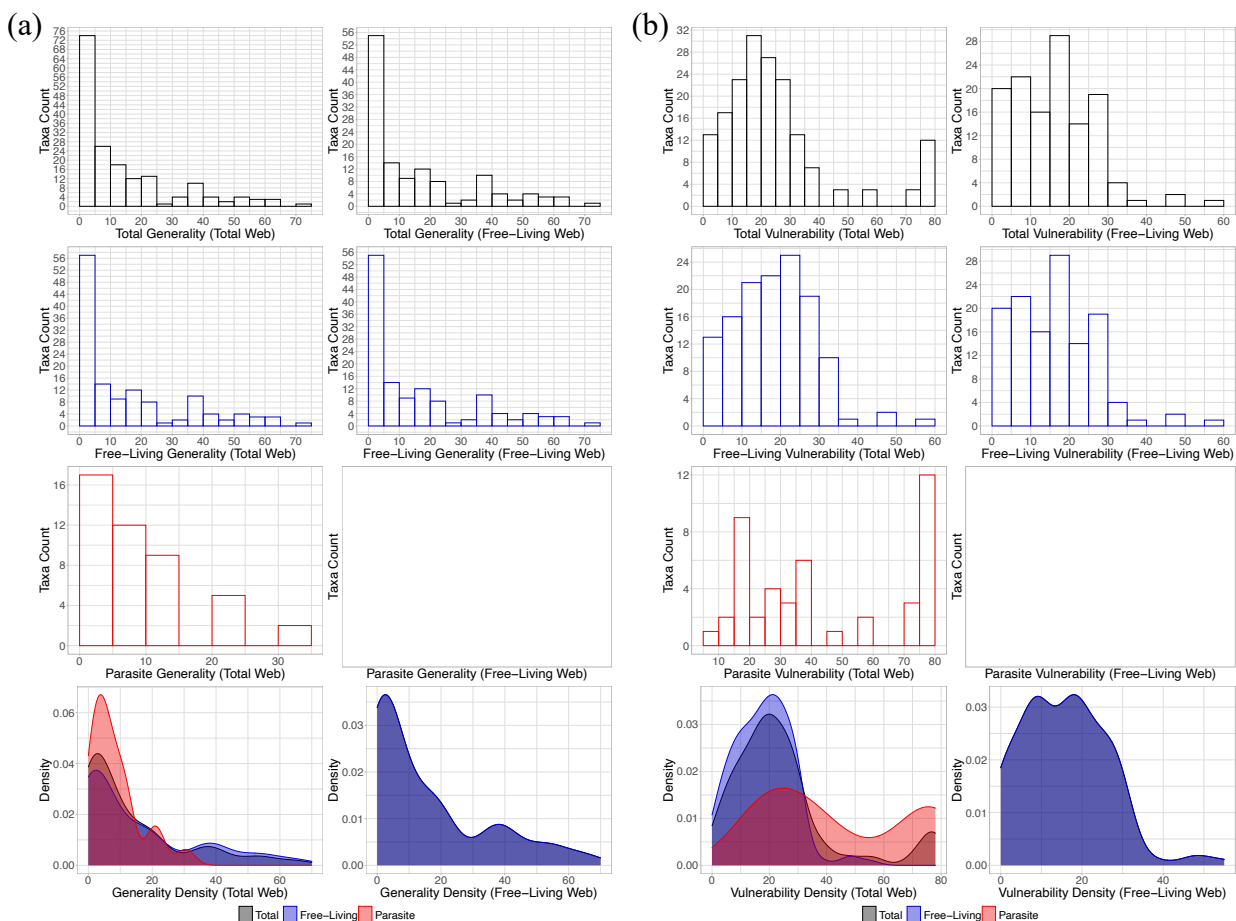


Figure 5. Histograms depicting (a) generality and (b) vulnerability distributions of the total web (left panel) vs the free-living web (right panel). Generality is further subdivided into generality of free-living nodes (prey taxa counts) and parasite nodes (host taxa counts). Vulnerability is further subdivided into vulnerability of free-living nodes (to predation and parasitism) and parasite nodes (to predation). Density plots of each web’s generality and vulnerability are overlaid for easier comparison.

Overall, the nodes in the total web were more connected than the nodes in the free-living web, due to the addition of the parasite taxa and their links (**Table 4**). In both webs, two of the most connected nodes were the lake's only amphipod *Gammarus lacustris* (free-living web = 82 links, total web = 128 links) and charr (free-living web = 78 links, total web = 139 links). While the other two fish species were also among the most connected nodes in the total web (stickleback = 123, trout = 115), they were the 7th and 10th most connected species in the free-living web (stickleback = 67, trout = 56) – a likely indication of how vulnerable to parasitism these two species are. Water mites were also highly connected in the total web with 131 reported links. The water mites are connected via links in the trophic network both as a parasitic and a free-living, predatory node. However, as the free-living web only includes the non-parasitic life stage of water mites, the number of links decreased to 68. In the free-living web, stickleback, trout, and water mites were replaced by two stone fly nodes, *Arcynopteryx compacta* (76 links) and *Diura bicaudata* (76), and the copepod, *Megacyclops gigas* (73) as the most connected taxa. While the connectedness of *A. compacta*, *D. bicaudata*, and *M. gigas* increased in the total web (104, 106, and 111 links respectively), they were not represented among the most connected species. The most general taxa remained the same between the two webs, except for one node that was represented by water mites in the total web and replaced by *Sialis lutaria* in the free-living web. The most vulnerable species were drastically different between the total and free-living webs with the total web's most vulnerable taxa consisting solely of parasites, specifically trematodes, and the free-living web's most vulnerable list made up of producers and Chironomidae (**Table 4**). In fact, all 17 trematodes in Takvatn were among the most vulnerable taxa in the total food web.

Table 4. Most connected taxa, most general taxa, and most vulnerable taxa in both webs. The number of links for each taxon are also included.

	Total Web	Links	Free-Living Web	Links
Most Connected	1 <i>Salvelinus alpinus</i>	139	<i>Gammarus lacustris</i>	82
	2 <i>Hydracarina</i>	131	<i>Salvelinus alpinus</i>	78
	3 <i>Gammarus lacustris</i>	128	<i>Arcynopteryx compacta</i>	76
	4 <i>Gasterosteus aculeatus</i>	123	<i>Diura bicaudata</i>	76
	5 <i>Salmo trutta</i>	115	<i>Megacyclops gigas</i>	73
Most General	1 <i>Salvelinus alpinus</i>	70	<i>Salvelinus alpinus</i>	70
	2 <i>Gammarus lacustris</i>	64	<i>Gammarus lacustris</i>	64
	3 <i>Arcynopteryx compacta</i>	64	<i>Diura bicaudata</i>	64
	4 <i>Diura bicaudata</i>	64	<i>Arcynopteryx compacta</i>	64
	5 <i>Hydracarina</i>	61	<i>Sialis lutaria</i>	57
Most Vulnerable	1 <i>Diplostomum</i> Lineage 3	78	<i>Detritus (allochthonous and autochthonous)</i>	55
	2 <i>Diplostomum</i> Lineage 4	78	<i>Tabellaria flocculosa (agg.)</i>	48
	3 <i>Diplostomum</i> Lineage 5	78	<i>Unidentified pennate diatoms</i>	48
	4 <i>Diplostomum</i> Lineage 6	78	<i>Unidentified coccal bluegreen algae</i>	38
	5 <i>Tylodelphys sp.2</i>	78	<i>Protanypus morio</i>	30
	6 <i>Apatemon gracilis</i>	78	<i>Abiskomyia sp. (virgo)</i>	30
	7 <i>Apatemon sp.1</i>	78	<i>Heterotrissocladius subpilosus</i>	30
	8 <i>Strigeinae gen sp</i>	78	<i>Heterotrissocladius marcidus</i>	30

3.2. Benthic Compartment vs. Pelagic Compartment

Among the 174 nodes making up the total food web, 53 taxa were assigned to the pelagic compartment and 128 taxa to the benthic compartment (**Table 5**). Seven taxa (three fishes, three birds, and a copepod) were recorded as members of both the pelagic and benthic compartments. The pelagic compartment consisted of 4.6 trophic levels with 12 basal species, 27 free-living predators, and 14 parasites, whereas the much larger benthic compartment had 4.7 trophic levels consisting of 23 basal species, 75 free-living predators, and 31 parasites (**Figure 6, Figure 7**). While the pelagic compartment's first trophic level was made up of phytoplankton, the benthic compartment's primary producers include detritus, periphyton, and macrophytes. The benthic compartment, with the highest number of nodes, also had the highest number of links (3281 vs 535) and a linkage density that was more than double that of the pelagic compartment (25.6 vs 10.1) (**Figure 8, Figure 9**). However, the connectance was similar for the two compartments, with the benthic having a slightly higher calculated value (benthic = 0.200, pelagic = 0.190). Parasitic taxa accounted for 26% of the nodes in the pelagic compartment and 23% in the benthic compartment, and parasitic links made up 61% of all trophic relationships in the pelagic and 48% in the benthic.

Table 5. Summary of calculated key topological food web metrics for the benthic compartment and the pelagic compartment.

Metrics	Benthic Compartment	Pelagic Compartment
Nodes	128	53
Observed Links	3281	535
Connectance	0.200	0.190
Linkage Density	25.63	10.09
Max Trophic Level	4.6	4.7
Mean Degree	51.27	20.19
SD Degree	26.85	10.89
Mean Generality	15.38	5.23
SD Generality	17.64	5.09
Mean Vulnerability	25.63	10.09
SD Vulnerability	17.84	7.11

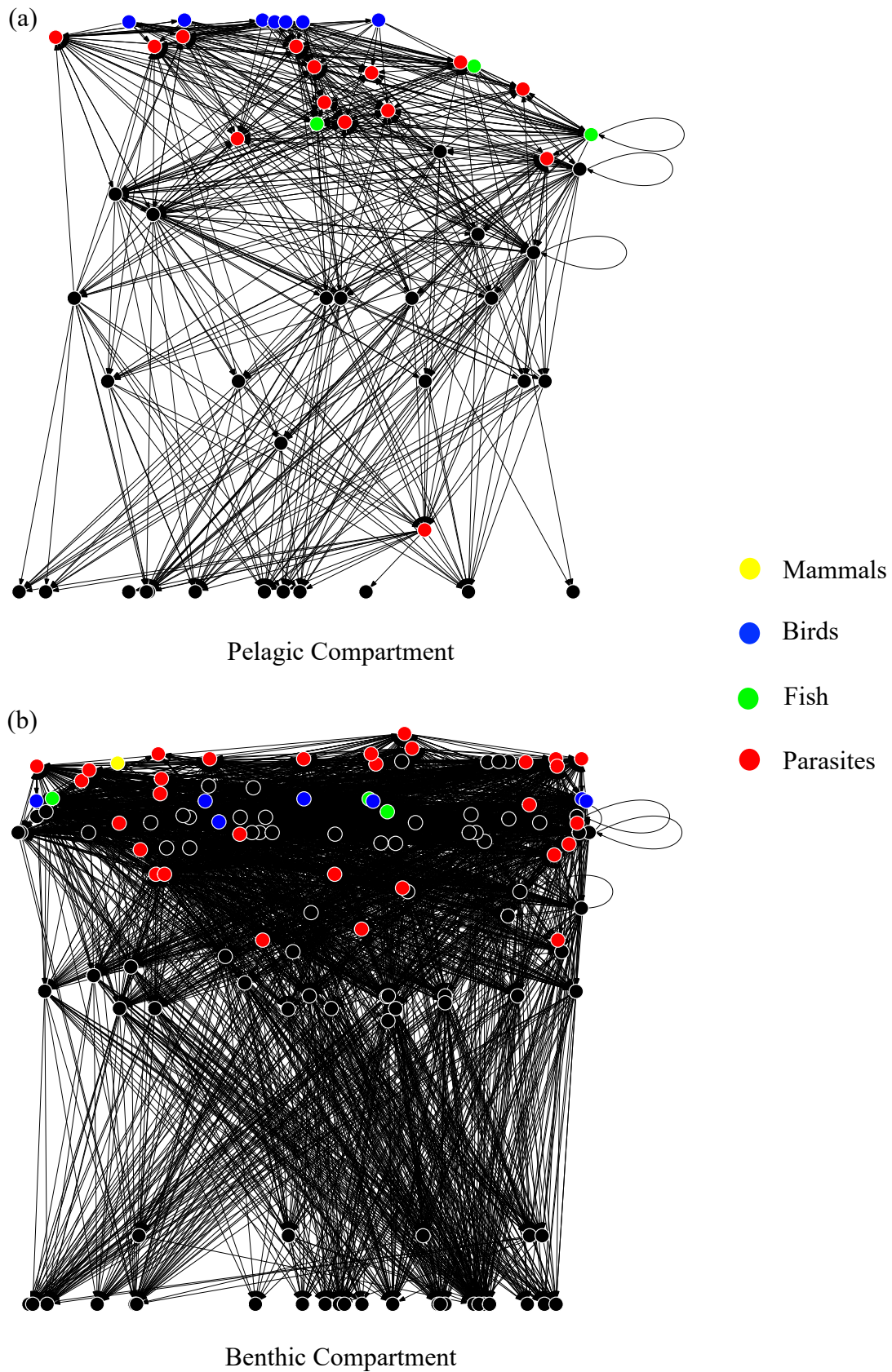


Figure 6. Food web of Takvatn's (a) pelagic and (b) benthic compartments. The single mammal (*N. vison*) is depicted in yellow. The bird taxa are depicted in blue. The fish species are depicted in green. The parasites are depicted in red.

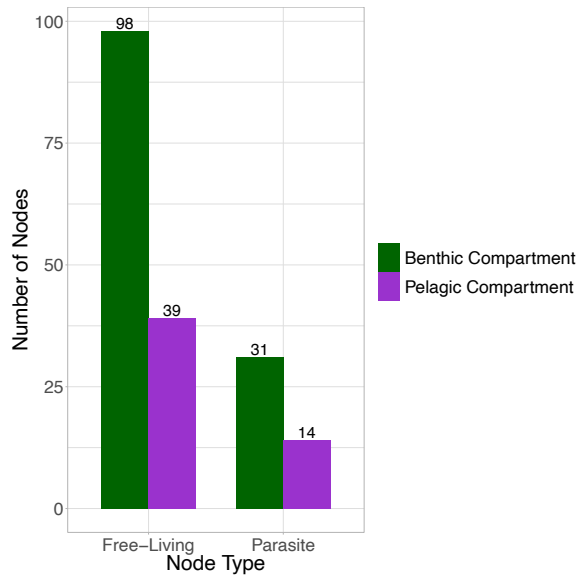


Figure 7. The total number of nodes in the benthic compartment and pelagic compartment divided into free-living nodes and parasitic nodes.

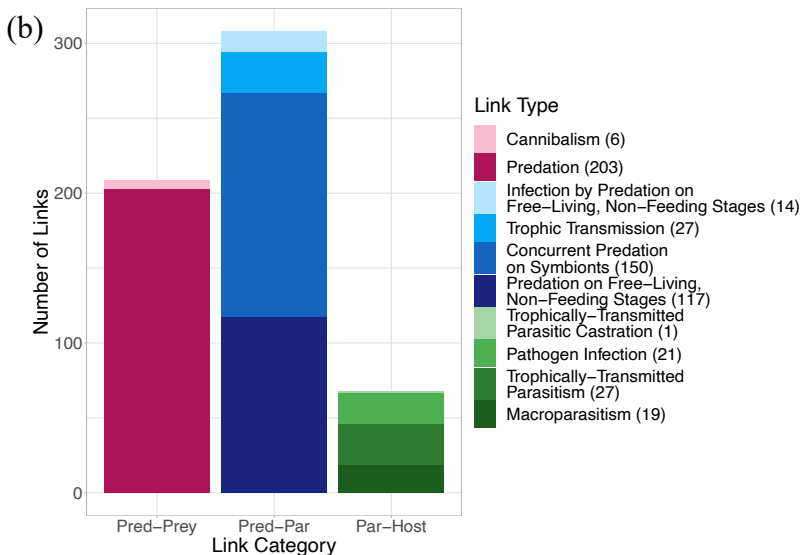
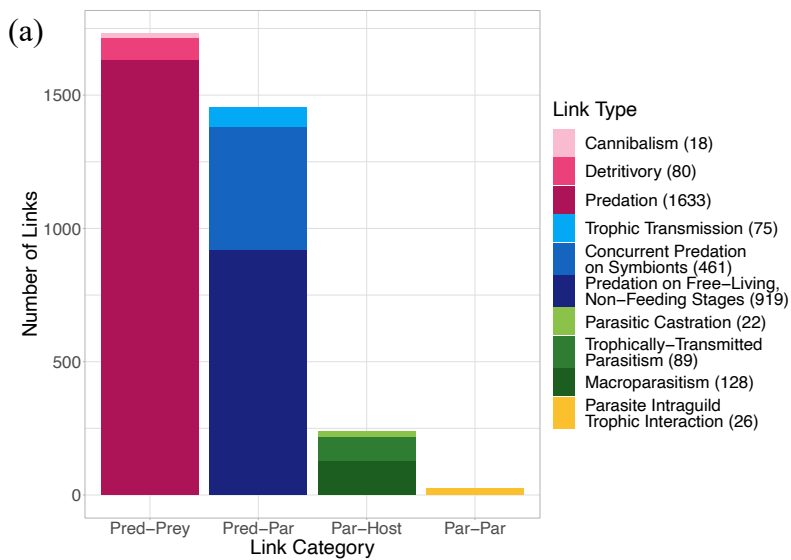


Figure 8. The number of links in (a) the benthic compartment and (b) the pelagic compartment. Each of the four link categories are subdivided into its corresponding link types. The number of links observed in each link type is presented in parentheses next to the link type name in the legend. The pelagic compartment did not contain any parasite-parasite links.

The benthic compartment of the total food web had a much higher mean generality than the pelagic (15.38 vs 5.23) (**Figure 9**). Both the free-living taxa and parasites had much higher mean generality in the benthic compartment than the pelagic compartment, suggestively due to the difference in size between the webs (**Figure 10a**). However, while the diet breadth of free-living taxa was double that of parasites in the benthic compartment (17.66 vs 8.52), the diet breadth of pelagic taxa was very similar, irrespective of taxa type (5.36 vs 4.86 for free-living and parasitic taxa, respectively). For both compartments, mean vulnerability was higher than mean generality (**Figure 9**). Taxa in the benthic compartment were much more vulnerable than their pelagic counterparts (25.63 vs 10.09), a result of the high mean free-living and mean parasite vulnerability. In fact, both benthic free-living taxa and benthic parasites were much more vulnerable than their pelagic counterparts (Free-Living: 19.83 vs 7.10; Parasites: 43.55 vs 18.43) (**Figure 10b**). However, in both compartments, parasites were observed to be much more vulnerable to their enemies than free-living taxa are (Benthic: 43.55 vs 19.83; Pelagic: 18.43 vs 7.10); Many free-living taxa were vulnerable to fewer enemies, while many parasites were vulnerable to many enemies (**Figure 10b**).

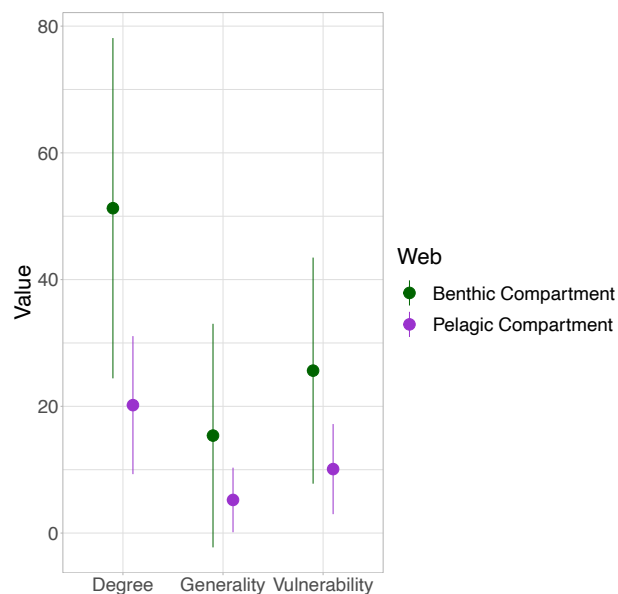


Figure 9. Mean degree, generality, and vulnerability and their respective standard deviations in the benthic compartment and pelagic compartment.

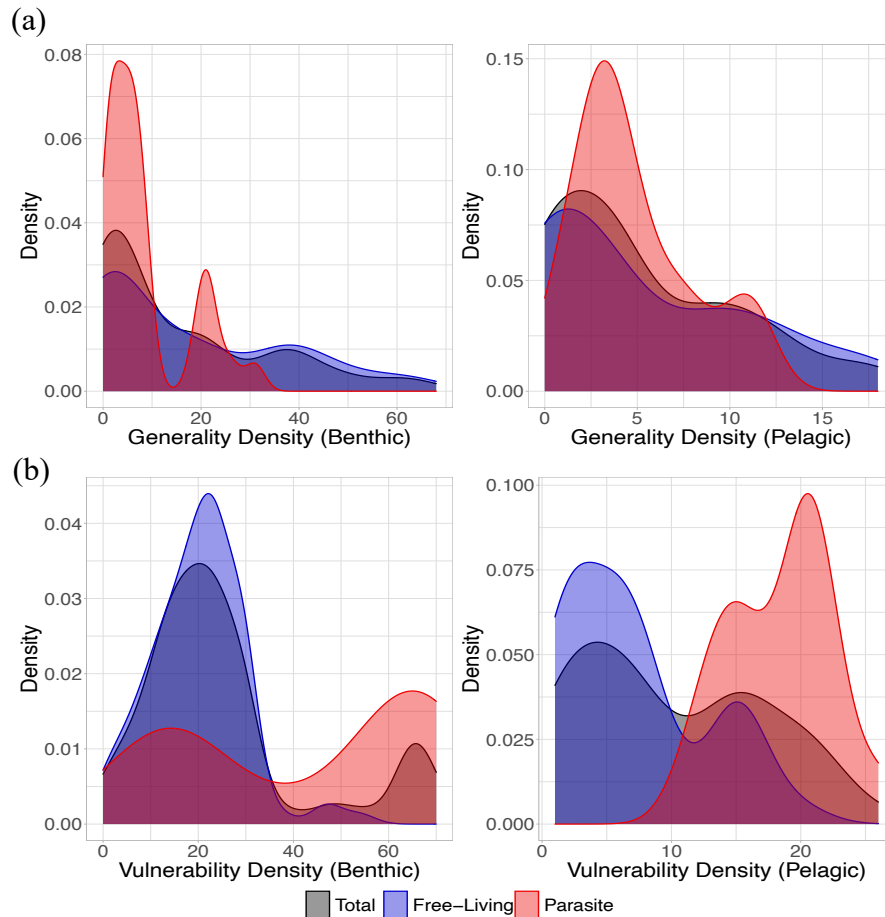


Figure 10. Density plots depicting (a) generality and (b) vulnerability distributions of the benthic compartment (left panel) vs the pelagic compartment (right panel).

Taxa in the benthic compartment each had more links to other nodes than taxa in the pelagic compartment (**Table 6**). The most connected benthic taxa, water mites, had 115 links to other benthic taxa. Again, the high number of reported links is likely due in part to water mites being linked as a taxon with both a parasite and a free-living stage. The amphipod *G. lacustris* was the second most connected species in the benthic web with 112 links. Charr were third with 105 links followed by the trichopteran *P. flavomaculatus* and the plecopteran *D. bicaudata* with 96 and 94 links, respectively. The most connected taxon in the pelagic web, the copepod *Eudiaptomus gracioloides*, had less than half the number of links as its counterpart in the benthic web (only 47 links). The next two most connected species were also copepods, *Cyclops scutifer* (46) and *H. appendiculata* (42). While stickleback was included in both webs, it was only among the most connected taxa in the pelagic web, where it was linked to 42 other nodes. While the stickleback was connected to 90 other nodes in the much larger benthic compartment, it was only the 8th most connected species in this compartment. Charr

was also found in both the benthic and pelagic webs, however while it only had 40 links in the benthic compartment, it was still among the most connected species in the web. For both compartments, the most vulnerable taxa consisted of parasites; parasitic trematodes in the benthic compartment and a parasitic oomycote and parasitic cestodes in the pelagic compartment.

Table 6. Most connected taxa, most general taxa, and most vulnerable taxa in the benthic compartment and the pelagic compartment. The number of links for each taxon are also included.

	Benthic Compartment	Links	Pelagic Compartment	Links
Most Connected	1 <i>Hydracarina</i>	115	<i>Eudiaptomus gracioloides</i>	47
	2 <i>Gammarus lacustris</i>	112	<i>Cyclops scutifer</i>	46
	3 <i>Salvelinus alpinus</i>	105	<i>Heterocope appendiculata</i>	42
	4 <i>Polycentropus flavomaculatus</i>	96	<i>Gasterosteus aculeatus</i>	42
	5 <i>Diura bicaudata</i>	94	<i>Salvelinus alpinus</i>	40
Most General	1 <i>Gammarus lacustris</i>	62	<i>Eudiaptomus gracioloides</i>	18
	2 <i>Diura bicaudata</i>	62	<i>Cyclops scutifer</i>	17
	3 <i>Arcynopteryx compacta</i>	62	<i>Bythotrephes longimanus</i>	17
	4 <i>Salvelinus alpinus</i>	61	<i>Heterocope appendiculata</i>	14
	5 <i>Hydracarina</i>	56	<i>Polyphemus pediculus</i>	13
Most Vulnerable	1 <i>Crepidostomum farionis</i>	70	<i>Saprolegnia spp.</i>	26
	2 <i>Allocreadium neotenicum</i>	70	<i>Dibothriocephalus dendriticus</i>	21
	3 <i>Crepidostomum metoecus</i>	69	<i>Dibothriocephalus ditremus</i>	21
	4 <i>Crepidostomum spp.</i>	69	<i>Schistocephalus solidus</i>	21
	5 <i>Cotylurus cornutus</i>	66	<i>Eubothrium crassum</i>	21
	6 –		<i>Eubothrium salvelini</i>	21

3.3. Post-Introduction Web vs. Pre-Introduction Web

The reconstructed pre-introduction food web was not only missing the two nodes representing the introduced fish species (charr and stickleback), but also 10 nodes of parasitic taxa that rely on charr or stickleback as hosts (**Table 7**). Additionally, the invasive mink was not included in the pre-introduction web, which had a total of 161 nodes (**Table 8, Figure 11**). These nodes were spread across 4.6 trophic levels as opposed to the 4.8 observed in the total web and included 35 basal nodes, 92 free-living predators, and 35 parasitic nodes (**Figure 12**). The introduction of the two fish species and their accompanying ten parasite taxa, along with the mink, also increased the number of links from 3613 to 4314, which led to an increase in linkage density, from 22.44 to 24.79, and a slight increase in connectance, from 0.139 to 0.142 (**Figure 13, Figure 14**).

Table 7. Thirteen taxa added to the Takvatn food web after 1930. Ten parasites relied on the introduced trout and stickleback. Additionally, the mink was not found in and around Takvatn until the 1980s.

Species	Node Type	Organismal Group
<i>Gasterosteus aculeatus</i>	Freeliving	Pisces
<i>Salvelinus alpinus</i>	Freeliving	Pisces
<i>Neovison vison</i>	Freeliving	Mammalia
<i>Gyrodactylus arcuatus</i>	Parasite	Monogenea
<i>Salmincola edwardsii</i>	Parasite	Copepoda
<i>Philonema oncorhynchi</i>	Parasite	Nematoda
<i>Cystidicola farionis</i>	Parasite	Nematoda
<i>Schistocephalus solidus</i>	Parasite	Cestoda
<i>Eubothrium crassum</i>	Parasite	Cestoda
<i>Eubothrium salvelini</i>	Parasite	Cestoda
<i>Proteocephalus filicollis</i>	Parasite	Cestoda
<i>Diplostomum</i> Lineage 4	Parasite	Trematoda
<i>Strigeinae gen sp.</i>	Parasite	Trematoda

Table 8. Summary of calculated key topological food web metrics for the post-introduction web and the pre-introductions web.

Metrics	Post-Introduction Web	Pre-Introduction Web
Nodes	174	161
Observed Links	4314	3613
Connectance	0.142	0.139
Linkage Density	24.79	22.44
Max Trophic Level	4.8	4.6
Mean Degree	49.59	44.88
SD Degree	30.83	27.66
Mean Generality	13.63	13.34
SD Generality	16.69	16.27
Mean Vulnerability	24.79	22.44
SD Vulnerability	19.12	18.30

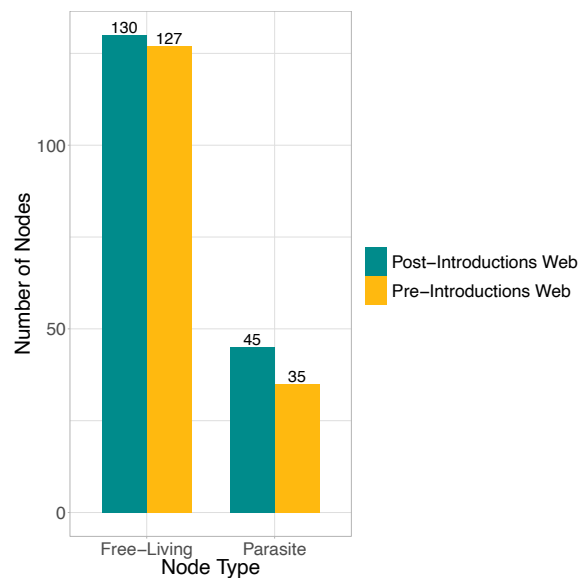


Figure 11. The total number of nodes in the web after the fish introductions and before the fish introductions divided into free-living nodes and parasitic nodes.

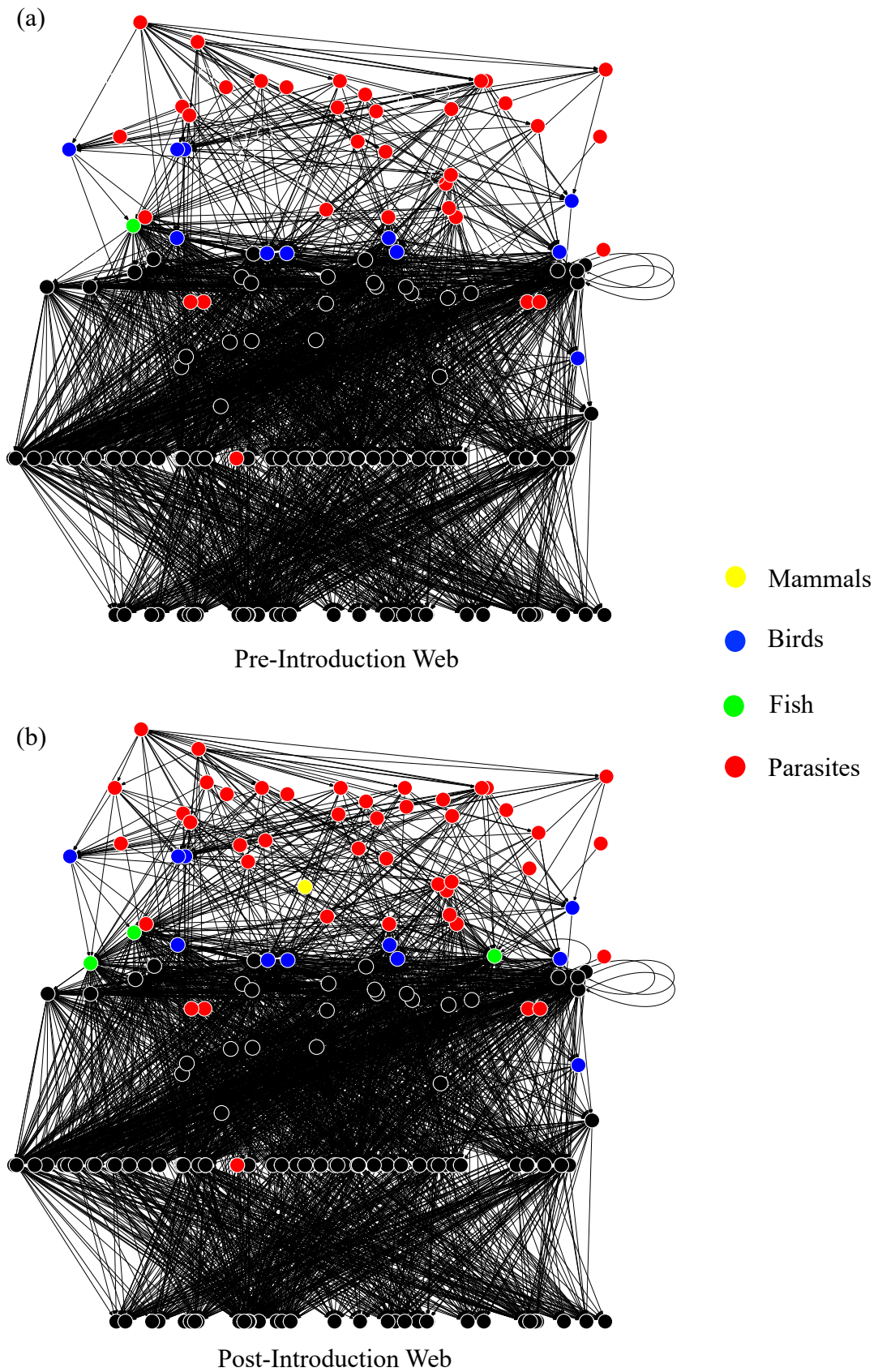


Figure 12. Takvatn's (a) pre-introduction and (b) post-introduction webs. The single mammal (*N. vison*) is depicted in yellow. The bird taxa are depicted in blue. The fish species are depicted in green. The parasites are depicted in red.

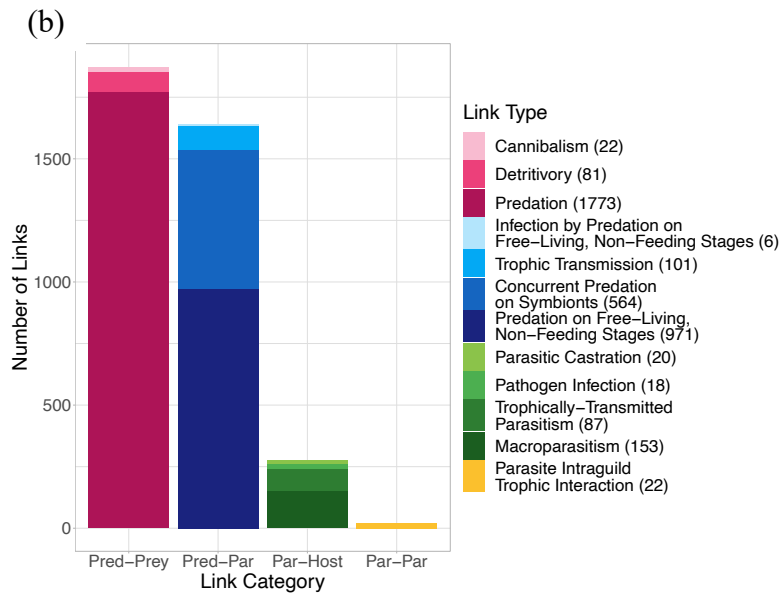
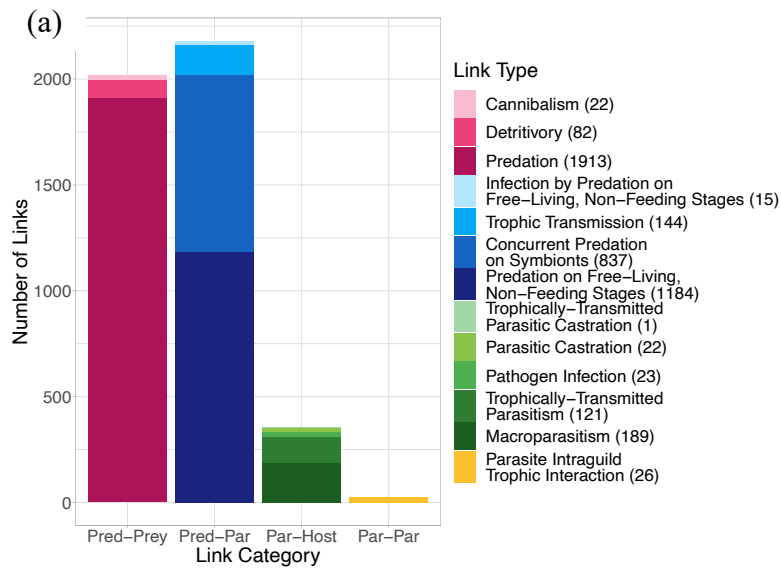
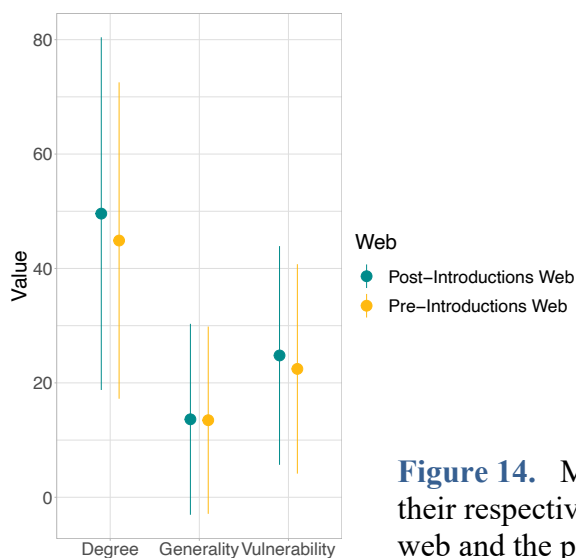


Figure 13. The number of links in (a) the post-introduction web and (b) the pre-introduction web. Each of the four link categories are subdivided into its corresponding link types. The number of links observed in each link type is presented in parentheses next to the link type name in the legend.



Prior to the species introductions, each node consumed or parasitized on average 13.34 prey and host taxa (**Figure 14**). This was nearly identical to the reported mean generality for taxa in the post-introduction web (13.63). Mean vulnerability was also similar, with taxa being vulnerable to an average of 22.44 enemies before the introductions and 24.79 enemies after the introductions. Additionally, before the introduction of charr and stickleback, on average, the free-living taxa consumed similar numbers of prey taxa as they did after the introductions (14.76 and 15.51, respectively) (**Figure 15a**). This pattern was also observed for mean parasite generality, with parasites consuming 8.54 taxa in the pre-introduction web and 8.46 in the post-introduction web. Mean vulnerability for both taxon types are also very similar in both time-steps of the web. Free-living taxa were vulnerable to 16.73 predators/parasites on average prior to the introductions and 18.18 predators/parasites on average after the introduction, while parasites were vulnerable to an average of 42.80 and 43.73 predators before and after the fish introductions, respectively (**Figure 15a**).

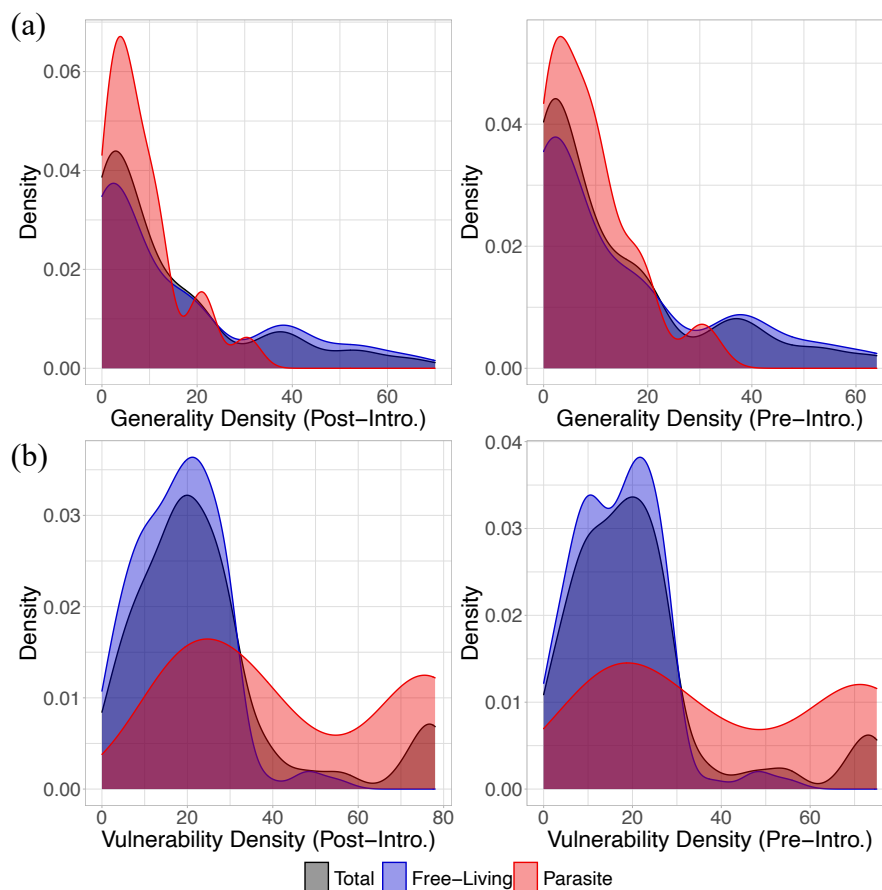


Figure 15. Density plots depicting (a) generality and (b) vulnerability distributions of the post-introduction web (left panel) and the pre-introduction web (right panel).

Taxa in the pre-introduction web were less connected than taxa in the post-introduction web (Table 9). However, the difference was not as large as revealed for the total and free-living webs. Water mites (119 pre-introduction vs 131 post-introduction), *G. lacustris* (116 vs 128), and trout (101 vs 115) were found to be among the most connected taxa both before and after the fish introductions. The stone fly *D. bicaudata* and the caddisfly *P. flavomaculatus* (both with 98 links) were also identified among the most connected taxa for the pre-introduction web, whereas the two introduced fish species, charr and stickleback, were highly connected in the post-introduction web with 139 and 123 links, respectively.

Table 9. Most connected taxa, most general taxa, and most vulnerable taxa in the post-introduction web and the pre-introductions web. The number of links for each taxon are also included.

	Total Web	Links	Total Pre-Introduction	Links
Most Connected	1 <i>Salvelinus alpinus</i>	139	<i>Hydracarina</i>	119
	2 <i>Hydracarina</i>	131	<i>Gammarus lacustris</i>	116
	3 <i>Gammarus lacustris</i>	128	<i>Salmo trutta</i>	101
	4 <i>Gasterosteus aculeatus</i>	123	<i>Diura bicaudata</i>	98
	5 <i>Salmo trutta</i>	115	<i>Polycentropus flavomaculatus</i>	98
Most General	1 <i>Salvelinus alpinus</i>	70	<i>Gammarus lacustris</i>	64
	2 <i>Gammarus lacustris</i>	64	<i>Arcynopteryx compacta</i>	64
	3 <i>Arcynopteryx compacta</i>	64	<i>Diura bicaudata</i>	64
	4 <i>Diura bicaudata</i>	64	<i>Hydracarina</i>	61
	5 <i>Hydracarina</i>	61	<i>Sialis lutaria</i>	57
Most Vulnerable	1 <i>Diplostomum Lineage 3</i>	78	<i>Diplostomum Lineage 3</i>	75
	2 <i>Diplostomum Lineage 4</i>	78	<i>Diplostomum Lineage 5</i>	75
	3 <i>Diplostomum Lineage 5</i>	78	<i>Diplostomum Lineage 6</i>	75
	4 <i>Diplostomum Lineage 6</i>	78	<i>Tylodelphys sp.2</i>	75
	5 <i>Tylodelphys sp.2</i>	78	<i>Apatemon gracilis</i>	75
	6 <i>Apatemon gracilis</i>	78	<i>Apatemon sp.1</i>	75
	7 <i>Apatemon sp.1</i>	78	<i>Trichobilharzia franki "peregra"</i>	75
	8 <i>Strigeinae gen sp</i>	78	–	

4. DISCUSSION

Incorporating parasites into Takvatn's food web allows for further insight into the structure and functioning of the food web and ultimately the whole system. Consistent with previous studies (Amundsen et al. 2009, Preston et al. 2014, Morton and Lafferty 2022) and the hypothesis put forward in the current study, these parasite additions resulted in an increase in most food web metrics measured for the total food web, including connectance, linkage density, and mean vulnerability. However, contrary to my predictions, mean generality was observed to decrease with the inclusion of parasitic nodes. The differences observed in network metrics between Takvatn's food web with and without parasites points to the important role parasites play in trophic interactions within a lake ecosystem. Separating the total food web into its pelagic and benthic compartments aided in discerning the topological role of parasites within the two compartments. In accordance with the hypothesis presented above, the two compartments had different values for most topological food web metrics, with the benthic compartment displaying much higher values for each metric, and yet connectance was similar between the two compartments. The deliberate introduction of charr in 1930 and stickleback in 1950 to Takvatn also provided the opportunity for ten parasite taxa to hitch along and establish themselves in the new ecosystem. In addition, mink had arrived at the lake at this time. However, while these additional nodes did increase linkage density and mean vulnerability, they had very little effect on the other measured key food web topology metrics.

4.1. Total Web vs. Free-Living Web

Connectance is expected to decrease with the inclusion of parasites because the addition of more nodes into a food web typically increases the number of potential links much faster than the number of observed links (Morton and Lafferty 2022). Nonetheless, connectance was observed to increase in the current analysis. Therefore, the changes in network metrics observed here are not an artifact of the increased network size with the addition of parasites but are indeed due to distinct characteristics of the parasites themselves. This increase means that the parasites, on average, have more links to other nodes than the free-living taxa have in Takvatn. Such an increase in connectance is contradictory with several previous analyses comparing food webs with and without parasites (Dunne et al. 2013, Preston et al. 2014). However, a similar increase in connectance was observed in the previous food web analysis in Takvatn focusing on the pelagic compartment (Amundsen et al. 2009), as well as in a salt

marsh food web (Lafferty et al. 2006). The increase in connectance observed in the total Takvatn food web was due to an increased mean vulnerability via the parasites' specialized trophic links – specifically the trophic interactions involving trematodes.

The higher mean vulnerability observed in parasites compared to free-living taxa was partially responsible for the increase in the total web's connectance. However, mean parasite generality did not contribute to the increased connectance observed in the total web. In fact, mean generality was higher in the free-living web, without the parasites included. This is likely because parasites were, on average, much more specialized than free-living taxa, even after considering the many parasite-host links that parasites introduced to the total web. These parasite-host trophic links also introduced new enemies for the free-living taxa and slightly increased their mean vulnerability. Furthermore, the addition of parasites also resulted in the addition of predator-parasite links. These links only served to further increase the vulnerability of parasite taxa. They did not increase the generality of free-living taxa because such links were not included in counts of free-living taxa generality since it is argued that they gain miniscule, if any, energetic value from consuming these typically tiny parasites and this consumption therefore has little effect on the web's flow of energy (Morton and Lafferty 2022). Additionally, since almost 50% of the links were categorized as predator-parasite, while only 8% of the links were categorized as parasite-host, mean parasite vulnerability was much greater than their mean generality, while the diet breadth and number of enemies of free-living taxa remained much more stable with and without parasites. This contributed to the overall increase in mean vulnerability and decreased mean generality observed in the total web.

Trematodes in particular are likely to contribute to the observed increase in connectance in the total web. According to the network that formed the basis for this analysis, Takvatn is home to 17 trematode taxa, all of which are among the most vulnerable taxa in the total web as well as the most general parasites in the total web with wide host breadths. Trematodes are also responsible for introducing the fourth link category, parasite-parasite, to the total web upon the inclusion of parasites. Larval trematodes often compete for space within a common snail intermediate host they are infecting (Kuris 1990, Lafferty et al. 1994). This results in intraguild predation, as one trematode will prey upon the other to eliminate the competition and utilize more of the snail's resources. In the Takvatn web, five trematode taxa participated in 26 parasite-parasite trophic interactions. This type of trophic interaction increases web

connectance by increasing the number of links among species within the same class. In addition, this served not only to increase the trematodes' vulnerability, but also the mean vulnerability of the total web. Accordingly, trematodes were the parasites with the most enemies in the food web. High trematode vulnerability was also the result of many trophic interactions in which free-living predators consumed free-living infectious larval trematodes (cercariae). In fact, over 80% of the "predation on free-living, non-feeding stages" links involved cercariae. Cercariae are released by their first intermediate hosts, mollusks, and use their brief 24-hour lifespan to seek out a suitable second intermediate host (Orlofske et al. 2015, McKee et al. 2020). Cercariae can be very abundant in lake ecosystems and offer a glycogen- and lipid-rich food source for many non-host taxa (McKee et al. 2020). Specifically, the cercariae of *Tylodelphys sp. 2* in Takvatn are consumed by rotifers, copepods, cladocerans, insect larvae, amphipods, gastropods, bivalves, oligochaetes, Hydracarina, and nematodes. These trophic interactions drastically increased the vulnerability of trematodes and resulted in an increase in the total web's mean vulnerability as well.

Some parasites' ability to alter the behavior or morphology of their host may also lead to increased connectance within the total web (Amundsen et al. 2009). Modifications are made to the host to increase the chances that the host is consumed, thereby increasing the chances that the parasite is able to infect the host necessary to fulfill its next lifecycle stage (Moore 2002, Thomas et al. 2005, Poulin 2010). Acanthocephalans are notorious host modifiers (Moore 1984, Lagrue et al. 2007, Franceschi et al. 2008, Benesh et al. 2009). One study showed that acanthocephalans exhibit olfactory-triggered manipulation to make their amphipod hosts prefer predator odors (Baldauf et al. 2007). Additionally, *Dibothriocephalus* cestodes, two of which inhabit Takvatn, are also known to manipulate their intermediate hosts to more efficiently reach their final host (Lafferty 1999). For example, *Dibothriocephala* infect copepods, and impede their predatory escape responses (Pasternak et al. 1995). This makes the copepods relatively easy prey for stickleback, for which they are a main food source (Folstad et al. 1994), and allows easier transmission of *Dibothriocephalus* between intermediate hosts. Consuming these copepods is also what provides male stickleback with their red coloration – a secondary sexual trait in these fishes (Folstad et al. 1994). However, the more colorful the stickleback is, the higher the risk of predation from birds, and therefore, the higher the chances of transmitting *Dibothriocephalus* to its final bird host (Jamieson 1994). Therefore, the addition of parasites, and especially nematodes, trematodes, cestodes, and acanthocephalans (Poulin 1994), could aid to increase connectance, mean parasite

vulnerability, mean free-living generality in the Takvatn web due to their unique characteristics as parasites.

Except for Hydracarina, which was not vulnerable to parasitism, all the most connected taxa in the total food web were also among the most parasitized taxa. *Gammarus lacustris*, the only amphipod in Takvatn was not only an important prey item for fish and birds, but also an important parasite host vulnerable to altogether nine parasite taxa. The amphipod was the most connected taxa in the free-living web and is therefore considered a hub within the food web that is able to connect parasites to their fish and bird final hosts (Shaw et al. 2020). The three fish species, stickleback, charr, and trout, were the most vulnerable to parasitism with 20, 19, and 16 links respectively. In fact, parasitism accounted for 63%, 70%, and 76% of their vulnerability, respectively and about 30% of the parasite taxa in Takvatn infect fish. The high level of parasitism experienced by these three fish species is partially due to their high level of connectance to other nodes in the Takvatn food web. In the free-living web, charr were the second most connected taxa in the web with 78 links and stickleback and trout were also well connected to other nodes in the web (67 and 56 links, respectively). Furthermore, both charr and trout were size-dependently piscivorous, with larger individuals consuming infected stickleback (Amundsen 1994, Klemetsen et al. 2003), and their positions in higher trophic levels also enhanced their vulnerability towards parasitism through trophic transmission (Timi et al. 2011). Larger-sized predators closer to the top of the food web typically have a wider diet breadth and ingest more prey items, providing a higher rate of exposure to infective trophically-transmitted parasitic stages. Additionally, trout and char in Takvatn are known to experience ontogenetic niche shifts in which smaller, younger fish feed on different prey taxa than larger, older fish, and thereby further increase their species diet breadth while simultaneously being exposed to different parasite taxa (Knudsen et al. 2008, Gallagher and Dick 2010, Henriksen et al. 2016, Prati et al. 2021).

The snail *Radix balthica*, although not very highly connected, was parasitized by 13 taxa, all of which were trematodes. Snails act as the obligatory first intermediate host for many digenetic trematodes, as it is within the snail host that the trematode completes its larval development (Littlewood and Bray 2000). However, the trematode larva does not require the snail host to be preyed upon to accomplish transmission and infect its next intermediate host. Rather, the trematode larva further develops into a free-living, non-feeding cercaria before leaving the snail and seeking out another suitable host to parasitize (Orlofske et al. 2015,

McKee et al. 2020). This could explain why even though *R. balthica* is vulnerable to parasitism from the highest number of parasitic taxa, it is not among the most connected taxa in Takvatn's food web. Additionally, even though they were not considered among the most connected taxa, the bird taxa were also heavily parasitized with 40% of all Takvatn's parasitic taxa infecting birds. Eight of the bird taxa were exceptionally vulnerable to parasites, each harboring between 11 and 15 parasite taxa. The birds are a common final host for many parasites with complex life cycles. This is likely related to the diet of the birds at Takvatn. All eleven bird taxa preyed upon *G. lacustris*, a highly parasitized species, as discussed above. Furthermore, all but two of the bird taxa also consumed stickleback, while many consumed all three heavily parasitized fish species.

Thirteen free-living taxa were only vulnerable to parasites, including all the bird species and two phytoplankton taxa. The two phytoplankton taxa *P. mougeotii* and *T. flocculosa* v. *geniculate* are not vulnerable to any herbivores because they are considered inedible. However, they are parasitized by chytrid fungi via a pathogen infection. Chytrids use chemotaxis to seek out hosts before penetrating the phytoplankton's cell (Frenken et al. 2017). Chytrids proceed to grow tubular rhizoids that extract the host's nutrients and produce motile zoospores to release into the water column (Sime-Ngando 2012, Frenken et al. 2017). These zoospores provide a highly nutritional food source for many zooplankton taxa, and could thereby aid in further connecting primary and secondary producers (Rasconi et al. 2014). Accordingly, chytrid infection in the two inedible filamentous phytoplankton in Takvatn actually allows zooplankton within the system to indirectly gain nutrition and energy from the phytoplankton by consuming chytrid zoospores.

4.2. Benthic Compartment vs. Pelagic Compartment

Connectance was expected to be lower in the much larger benthic compartment relative to the pelagic compartment as an artifact of their differences in matrix size (Morton and Lafferty 2022). Additionally, the benthic compartment included specific taxa that were expected to further decrease the compartment's connectance. For example, the very host specific gregarines are found in the benthic compartment. Gregarines are macroparasites and have direct lifecycles within a single host, thereby inhibiting connectance. In Takvatn, the eight gregarine taxa infected an average of less than two hosts. Additionally, the two top predators in the system, the mink and the single leech species, as well as most of the primary producers and other basal species were found in the benthic compartment. These nodes have no links in

one direction (not fed upon in the case of the top-predators and non-feeding in the case of the basal species), and therefore may aid in further decreasing connectance. The above factors were expected to result in a much lower connectance in the benthic compared to the pelagic compartment.

However, in contrast to the expected differences in connectance between the benthic and pelagic compartments, this analysis found that the two compartments had very similar connectance. In general, the benthic nodes had a larger diet breadth and more enemies than nodes in the pelagic compartment. For example, while the leech (*Glossiphonia complanata*) was a top predator with zero trophic interactions in which it participated as the prey, this species' generality was three times as high as the total benthic compartment's mean generality. Such a high level of generality provides more links between nodes, more than would be expected in such a large food web, as more specialists are expected to be present in larger networks (Dunne et al. 2002). This trend ultimately contributes to the higher-than-expected connectance observed in the benthic compartment. It has also been suggested that a network's connectance depends on the life history strategy of the parasites included in the web (Lafferty et al. 2006) and that parasites with higher host specificity may contribute to a lower connectance (Memmott et al. 2000). It can also be assumed that the same is true in respect to vulnerability: Parasites with fewer enemies may contribute to a lower connectance. In the Takvatn food web, on average, benthic parasites exhibited twice the diet breadth as their pelagic counterparts while also exhibiting over twice as many enemies as their pelagic counterparts, thereby serving to increase connectance. One group that may once again be partially responsible for this higher connectance in the benthic compartment are the trematodes. All the trematodes were in the benthic web and were identified as the most vulnerable taxa in the benthic compartment. As discussed earlier, this is likely partially due to their participation in intraguild predation (Kuris 1990, Lafferty et al. 1994). Furthermore, as discussed above, trematodes have an especially vulnerable infectious life stage during which they are free-living outside of their hosts (Orlofske et al. 2015, McKee et al. 2020). The benthic compartment contained almost five times as many predator-parasite links, mostly due to the presence of trematodes in the benthic compartment. Trophic interactions involving the predation of trematode cercariae made up almost 60% of all predator-parasite links in the benthic compartment. The presence of these trematode cercariae and the trophic links involving them greatly increase the parasites' mean vulnerability, and therefore the mean

vulnerability of the benthic compartment. This may ultimately lead to the higher-than-expected connectance observed in this compartment.

Furthermore, mean generality and mean vulnerability are metrics that depend on the size of the matrix in terms of the number of nodes. Therefore, the larger mean generality and mean vulnerability observed in the benthic compartment could merely be the result of a larger network size than the pelagic compartment. With such a large disparity in size between the two compartments, it is difficult to conclude how parasites are affecting the food web. The pelagic compartment of the Takvatn web only contained 14 parasites in this analysis, while the benthic contained 30 parasites. More analyses that control for increased network size by simulating food webs with the same size and connectance should be conducted (Williams and Martinez 2000, Morton and Lafferty 2022). Such further analyses can aid in understanding if the increases in connectance, mean generality, and mean vulnerability are higher than predicted by network size.

4.3. Post-Introduction Web vs. Pre-Introduction Web

The introduction of a species to a new ecosystem often provides the opportunity for parasites to hitch hike along and establish in the new ecosystem (Britton 2013, Lagrue 2017). Takvatn gained ten additional parasites that rely on charr or stickleback as hosts. Eight of these parasites were trophically transmitted and used the fish species as intermediate or final hosts, whereas two of them exhibited direct life cycles within either charr or stickleback (*Salmincola edwardsii* and *Gyrodactylus arcuatus*, respectively). Upon introduction to Takvatn along with the introduced fish hosts, the trophically-transmitted parasites host-switched and began spilling over and infecting other free-living taxa present in Takvatn to fulfill their lifecycles and establish future generations (Britton 2013). *Eubothrium crassum*, introduced with the stickleback, went on to further infect trout within Takvatn (Lian 2021). However, after its introduction, *E. salvelini* was not able to infect trout even though it was found to infect the prey items of trout. Furthermore, stickleback infected with *Schistocephalus solidus*, *Proteocephalus longicollis*, *Diplostomum* lineage 4, and *Strigeinae* gen sp. were also consumed by birds present at Takvatn, thus transmitting their infections to those taxa. All the trophically-transmitted parasites that were introduced with the two fish species also began their lifecycles anew in Takvatn and found suitable first intermediate hosts in four copepods, an amphipod, and two gastropods. The effects of such novel infections are likely to be widespread, as *E. crassum* infections in fish modify the host's appetite, potentially leading to

community level impacts (Bosi et al. 2005). Such a phenomena of parasite spillover was also reported in the European eel *Anguilla anguilla* due to the introduction of a Japanese eel, *Anguilla japonica*, which is infected with the nematode parasite *Anguillicoloides crassus* (Kennedy and Fitch 1990, Kirk 2003). *Anguilla japonica* was introduced to Europe through the aquaculture trade. This also led to the concurrent introduction of its nematode parasite. The introduced parasite was able to reproduce and infect native crustaceans as intermediate hosts, which were eventually consumed by the native eel allowing for the parasite to host-switch and successfully establish in *A. anguilla*. While *A. crassus* has little impact on its original eel host, it may impair spawning migration behavior and increase mortality rates in its new native host (Kirk 2003). Further studies should be conducted to elucidate the impact of Takvatn's introduced parasite taxa on community structure and free-living functional roles within the lake.

Not only did the introduced parasites spill over into other free-living taxa already present in Takvatn, but the two introduced fish species also acquired novel parasites when they consumed prey infected by native trophically-transmitted parasites in Takvatn. This may be the case for the trematode *Crepidostomum farionis* which infected trout as its final host prior to the fish introductions. After the fish introductions, *C. farionis* can now also be found infecting charr and stickleback. Kuhn et al. (2015) reported that the stickleback community of Lake Sagelvvatn, the lake from which the stickleback were introduced to Takvatn, was not vulnerable to infection by *C. farionis*. This is significant because Sagelvvatn is also inhabited by charr and trout, both of which were observed to harbor *C. farionis*. Therefore, it can be concluded that the stickleback population in Takvatn became infected with *C. farionis* by consuming parasitized copepods only after their introduction to Takvatn. Yet, it is still unclear why stickleback in Sagelvvatn were not parasitized by *C. farionis*, while stickleback in Takvatn are. This may have to do with diet and prey availability in the two lakes, but further studies should be conducted to resolve this. In this system, parasite spillback would only occur if an invading fish, infected with a native parasite, was consumed by a native fish (trout) or bird, thereby infecting that predator with a native parasite it had not been exposed to before (Lagrue 2017, Chalkowski et al. 2018, Llopis-Belenguer et al. 2020). However, there was no evidence of parasite spillback in the total Takvatn food web. This is likely because the native trout were already infecting the bird taxa via trophic transmission with all the native parasite taxa present in Takvatn prior to the introduction of the two other fish species.

These additional nodes and their links did not have a large impact on the overall connectance of the food web. The stability of connectance with the introduction of thirteen new taxa results from most of the added taxa having more links connecting them to other nodes than the taxa already established in Takvatn before the introductions. In fact, while connectance was expected to decrease slightly due to the addition of nodes, it was observed to increase. The introduction of stickleback is likely the main factor responsible for the slightly increased connectance. As stickleback are an efficient zooplankton predator, trophically-transmitted parasites infecting copepods as intermediate hosts were able to exploit this new host (Amundsen et al. 2013). However, not all such native parasites use the stickleback as an energetic resource. Such is the case for *Philonema oncorhynchi*, which uses stickleback as a paratenic host (Braicovich et al. 2016). Paratenic hosts do not serve to further the development of a parasite, but rather aid in the transmission of that parasite and bridge trophic gaps within a web through parasitic infections (Braicovich et al. 2016). The introduction of stickleback in Takvatn also introduced a new intermediate size class in the pelagic compartment of the lake, one that is more easily preyed upon by larger trout individuals (Amundsen et al. 2013). In fact, they are the dominant prey for large trout in Takvatn (Prati et al. 2021). Thus, stickleback have the potential to serve as paratenic hosts for parasites aiming to parasitize the higher trophic levels, i.e., the fish and birds in Takvatn. Specifically, the stickleback acts as a paratenic host to ensure higher transmittability of *P. oncorhynchi* to charr. Such trophic interactions that seek to increase the transmission of parasites also aid in increasing the connectance of the food web. Furthermore, connectance may have been slightly higher in the total web due to the introduction of parasites that alter their hosts' behavior. For example, *S. solidus* use stickleback as their second intermediate host, and to increase the chance that their fish host is consumed by a bird (which acts as this species' final host), *S. solidus* impairs the stickleback's anti-predator escape behavior (Barber et al. 2004). This phenotype manipulation aids in linking parasites and their free-living hosts to each other and may also facilitate the trophic transmission of other parasites that have a similar life cycle, for example *Dibothriocephalus* spp. (Amundsen et al. 2009, Amundsen et al. 2013).

Despite these new parasite-related links being added to the total Takvatn food web with the addition of the two fishes, most of the measured food web metrics remained quite stable. Only linkage density and mean vulnerability were observed to change. Even though the increase in mean vulnerability was not as dramatic as the difference observed between the Takvatn web with and without parasites, it is still noteworthy. These new nodes introduced 538 new

predator-parasite links, a 33% increase in the number of this link type. As discussed above, predator-parasite links introduce more vulnerability than generality since these trophic interactions are not counted in a taxon's generality because it is argued that they gain miniscule, if any, energetic value from consuming these typically tiny parasites and has little effect on the web's flow of energy (Morton and Lafferty 2022). Therefore, these additional links only served to increase mean parasite vulnerability. Additionally, the new nodes increased parasite-host links by 28%. While these additional links increased parasite mean generality, they also further contributed to the web's increasing mean vulnerability by increasing the number of enemies that free-living taxa encounter. Furthermore, the two new trematodes were among the most vulnerable taxa in the total food web after the fish introductions, with a mean vulnerability three times higher than the average web vulnerability, thereby also increasing the total web's vulnerability.

The introduced parasites are not believed to have been present in Takvatn prior to the fish introductions as they cannot utilize trout as hosts (Bråten 1966, Scholz 1999, Scholz et al. 2003). However, a recent study concluded that while they can infect trout, *E. crassum* are not able to maintain infective levels of populations without stickleback (Lian 2021). While trout can become parasitized when feeding on infected copepods, copepods are not considered common prey for trout. Only when the trout feed on infected stickleback, which are much more common prey, can *E. crassum* ensure enough transmission to maintain established infective populations. Therefore, the cestode's prevalence and abundance chiefly increase in lakes with stickleback (Lian 2021). Additionally, there are some bird parasites that may have arrived in Takvatn prior to the fish introductions via the bird hosts moving from lake to lake and transporting their parasites with them (Kuhn et al. 2015). However, such transmission pathways can be neither confirmed nor denied with the available data. This analysis functioned under the pretense that only those species relying on charr and/or stickleback were not present in Takvatn's total food web prior to the fish introductions.

Additionally, the post-fish introductions food web also includes a node representing mink. However, even though mink are top predators within the system, they have a relatively narrow diet breadth consisting of only fish and fish carrion. While they participate in concomitant predation due to the parasites infecting their fish prey, this food web does not recognize any parasite-host links between parasites and mink, further decreasing their connectance to the web. Therefore, the inclusion of mink in Takvatn's food web did not

significantly impact key topological metrics. However, it is very likely that mink may be infected with fish parasites, particularly *Dibothriocephala*, when considering their diet and how general this parasite taxa is (Dick et al. 2001, Torres et al. 2004).

The results of the current study confirm the conclusions drawn from the previous food web analysis examining the effect of the fish introductions in Takvatn on its food web topology (Amundsen et al. 2013). The introduction of the two fish species impacted the web beyond the additional trophic interactions of charr and stickleback by also aiding in establishing ten additional parasite taxa that proceeded to infect the native invertebrates, fish, and bird taxa in the lake system. Almost 20 years and thousands of hours of field work and literature reviews later, we now have a more complete diet data set, which allowed for a more accurate analysis of how the introduced taxa altered food web structure and functioning, with values of connectance and linkage density better representing Takvatn's food web.

5. CONCLUSIONS

We know parasites are key species for ecosystem functioning and tightly woven within food webs. Therefore, it is vital to discern the impact parasites may have on trophic interactions and ecosystem structure, functioning, and stability within a freshwater system. The results from the current study demonstrate the ability of parasites to alter an entire lacustrine ecosystem due to their unique characteristics as parasites. Links involving parasites account for over half of all trophic interactions in the total Takvatn web, and similar patterns are seen in other studies across various ecosystems (Morton and Lafferty 2022). Therefore, it is clear that such taxa, especially trophically-transmitted parasites, play a large role in the structuring and functioning of the system and must be integrated into food webs. Especially when considering the role of both the benthic and pelagic compartments in the functioning of the total system, it is important to account for each compartment's parasite taxa and the impact they have on trophic interactions within the compartments. Additionally, when discerning the impact of introduced species, it is vital to also consider the parasites they may be bringing with them, and how those parasites could potentially effect change in key topological metrics, thereby impacting the structure and function of the network.

The inclusion of parasites in food web analysis aids in developing a more complete picture of the system and how it functions. With the analysis of solely the free-living network of an ecosystem, we might not fully understand the impacts of climate change, pollution, management programs, exploitation, or species introductions and extinctions (Lafferty et al. 2008). Therefore, by gaining a more thorough understanding of how parasites interact within the food web to affect system structure and functioning, we can better expect to accurately evaluate and mitigate such scenarios.

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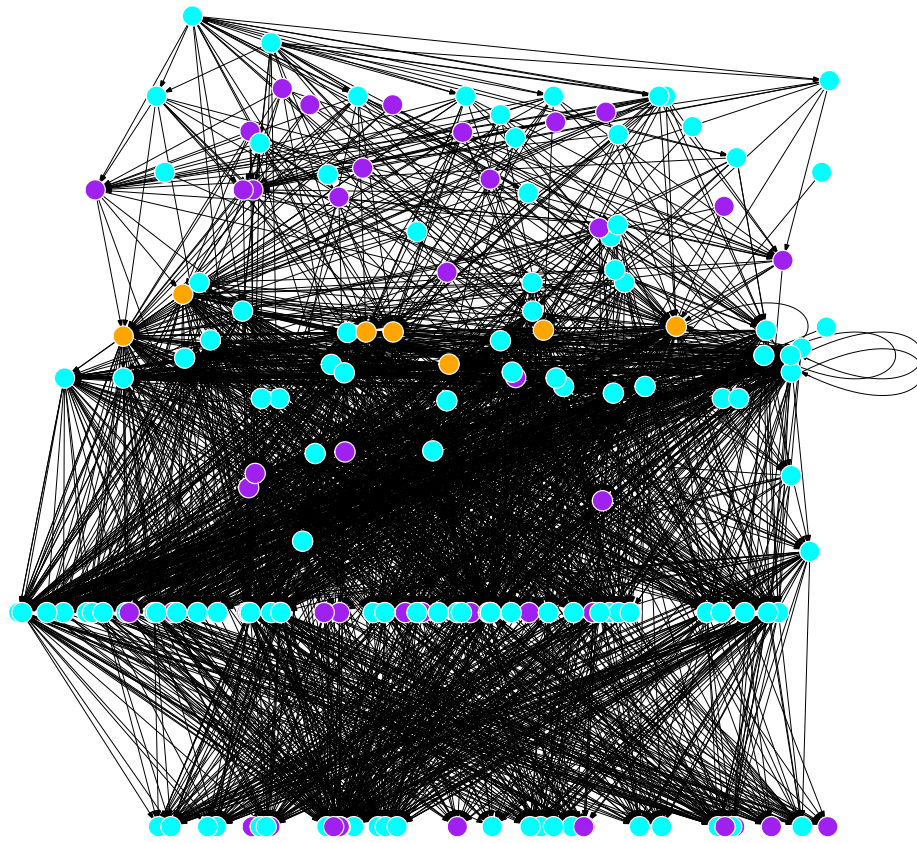
APPENDIX

Table S1. Summary of the four link categories (consumer-resource) and the 13 link types observed in each version analyzed of the Takvatn food web.

Link Category (Consumer-Resource)	Link Type	Total Web	Free-Living Web	Benthic Compartment	Pelagic Compartment	Pre-Introduction Web
Predator-Prey	Predation	1913	1913	1633	203	1773
	Detritivory	82	82	80	0	81
	Cannibalism	22	22	18	6	20
Predator-Parasite	Predation on Free-Living, Non-Feeding Stages	1184	0	919	117	971
	Concurrent Predation on Symbionts	837	0	461	150	564
	Trophic Transmission	144	0	75	27	101
	Infection by Predation on Free-Living, Non-Feeding Stages	15	0	0	14	6
Parasite-Host	Macroparasitism	189	0	128	19	153
	Trophically-Transmitted Parasitism	121	0	89	27	87
	Pathogen Infection	23	0	0	21	18
	Parasitic Castration	22	0	22	0	20
	Trophically-Transmitted Parasitic Castration	1	0	0	1	0
Parasite-Parasite	Parasite Intraguild Trophic Interaction	26	0	19	0	22

Table S2. Thirteen taxa added to the Takvatn food web after 1930, including their degree, generality, and vulnerability in the total food web. Ten parasites relied on the introduced trout and stickleback. Additionally, the mink was not found in and around Takvatn until the 1980s.

Species	Node Type	Degree	Generality	Vulnerability	Organismal Group
<i>Gasterosteus aculeatus</i>	Freeliving	123	55	32	Pisces
<i>Salvelinus alpinus</i>	Freeliving	139	70	27	Pisces
<i>Neovison vison</i>	Freeliving	27	4	0	Mammalia
<i>Gyrodactylus arcuatus</i>	Parasite	39	1	38	Monogenea
<i>Salmincola edwardsii</i>	Parasite	28	1	27	Copepoda
<i>Philonema oncorhynchi</i>	Parasite	36	4	32	Nematoda
<i>Cystidicola farionis</i>	Parasite	20	2	18	Nematoda
<i>Schistocephalus solidus</i>	Parasite	33	7	26	Cestoda
<i>Eubothrium crassum</i>	Parasite	43	5	38	Cestoda
<i>Eubothrium salvelini</i>	Parasite	46	7	39	Cestoda
<i>Proteocephalus filicollis</i>	Parasite	36	4	32	Cestoda
<i>Diplostomum</i> Lineage 4	Parasite	88	10	78	Trematoda
<i>Strigeinae gen sp.</i>	Parasite	88	10	78	Trematoda



Total Post-introduction Web

● Benthic ● Pelagic ● Benthic and Pelagic

Figure S1. Total food web of Takvatn divided into its benthic (blue) and pelagic (purple) nodes. Seven taxa (orange) are found in both the benthic and pelagic compartments.

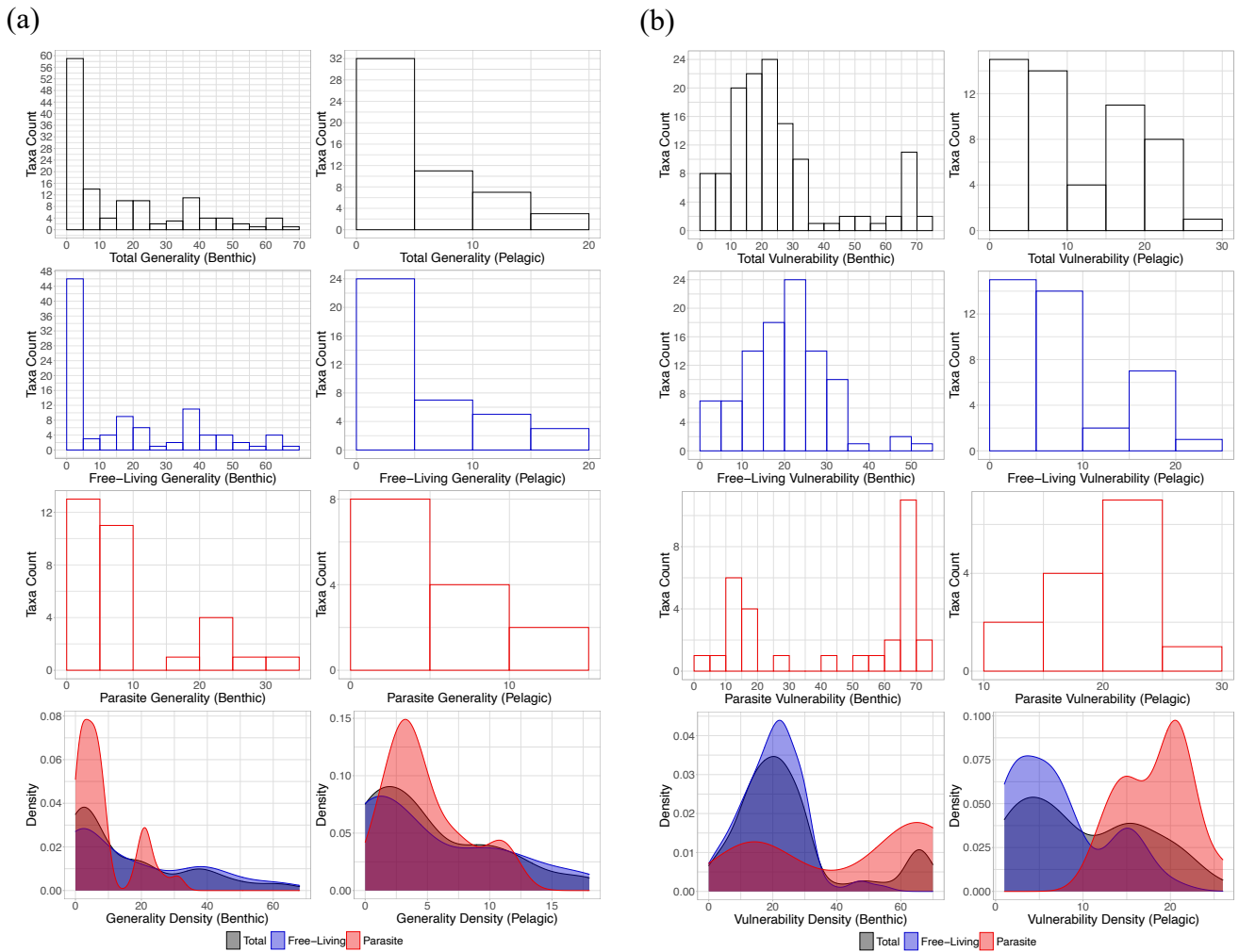


Figure S2. Histograms depicting (a) generality and (b) vulnerability distributions of the benthic compartment (left panel) vs the pelagic compartment (right panel). Generality is further subdivided into generality of free-living nodes (prey taxa counts) and parasite nodes (host taxa counts). Vulnerability is further subdivided into vulnerability of free-living nodes (to predation and parasitism) and parasite nodes (to predation). Density plots of each compartment's generality and vulnerability are overlaid for easier comparison.

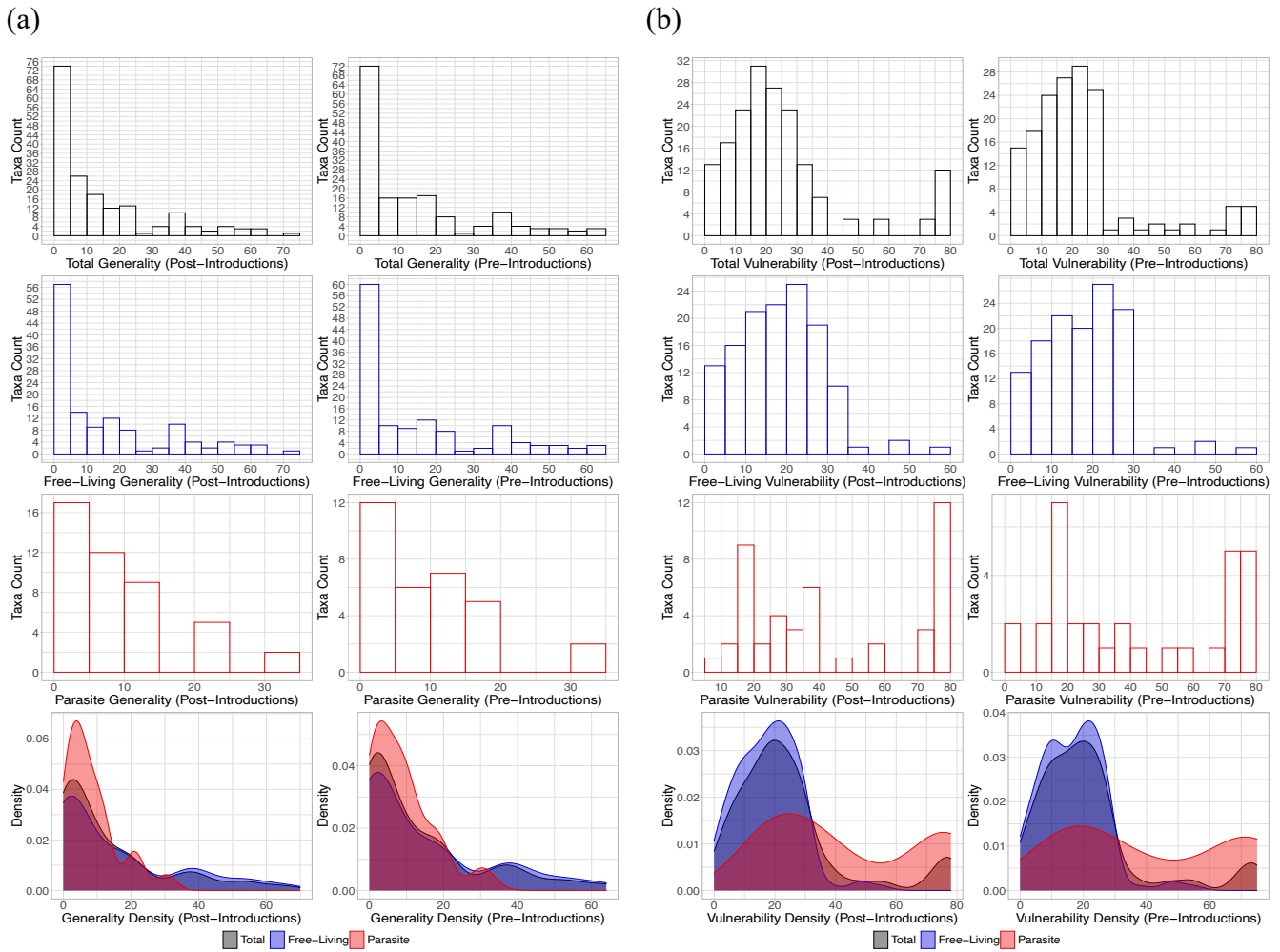


Figure S3. Histograms depicting (a) generality and (b) vulnerability distributions of the post-introduction web (left panel) and pre-introductions web (right panel). Generality is further subdivided into generality of free-living nodes (prey taxa counts) and parasite nodes (host taxa counts). Vulnerability is further subdivided into vulnerability of free-living nodes (to predation and parasitism) and parasite nodes (to predation). Density plots of each compartment's generality and vulnerability are overlaid for easier comparison.

