

## ARTICLE

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# Emergent trophic interactions following the Chinook salmon invasion of Patagonia

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**Abstract**

In their native range, Pacific salmon (*Oncorhynchus* spp.) have strong interactions with a multitude of species due to the annual pulse of marine-derived nutrients that they deliver to streams and forests when they spawn and die. Over the past few decades, Chinook salmon (*Oncorhynchus tshawytscha*) has established non-native populations throughout the Patagonia region of southern South America. Here, we provide the first assessment of the pathways through which salmon-derived nutrients enter stream and forest food webs in Patagonia by surveying multiple streams in southern Chile to identify invertebrate and vertebrate consumers of salmon carcasses and summarizing all documented trophic interactions of Chinook salmon in Patagonia. Blowflies (Calliphoridae) were the dominant colonizer of carcasses in the riparian zone, and midge flies (Chironomidae) were the most common invertebrate on submerged carcasses. Camera trap monitoring in the riparian zone revealed consumption of carcasses or carcass-associated invertebrates by the insectivorous passerine bird “chucáo” (*Scelorchilis rubecula*), small rodents (black rat *Rattus rattus*, house mouse *Mus musculus*, and/or colilargo *Oligoryzomys longicaudatus*), the South American fox “culpeo” (*Lycalopex culpaeus*), and the invasive American mink (*Neovison vison*). A mink was filmed transferring a carcass from stream to streambank, indicating that vertebrate scavenging likely increases the degree to which marine-derived nutrients enter terrestrial food webs. The native taxa that consume salmon are closely related to species that benefit from salmon consumption in North America, suggesting that the pathways of salmon nutrient incorporation in North American food webs have functionally re-emerged in South America. Similarly, non-native trout (*Oncorhynchus mykiss* and *Salmo trutta*) and mink consume salmon in Patagonia, and their eco-evolutionary history of coexistence with salmon could mean that they are preadapted for salmon consumption and could thus be key beneficiaries of this invasion. Expanded monitoring of the

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abundance and impacts of salmon will be vital for understanding how these novel inputs of marine-derived nutrients alter Patagonian food webs.

#### KEYWORDS

anadromous fish, camera trap, Diptera, galaxiid, invasional meltdown, invasive species, mink, nutrient subsidy, *Oncorhynchus*, trophic cascade, trout

## INTRODUCTION

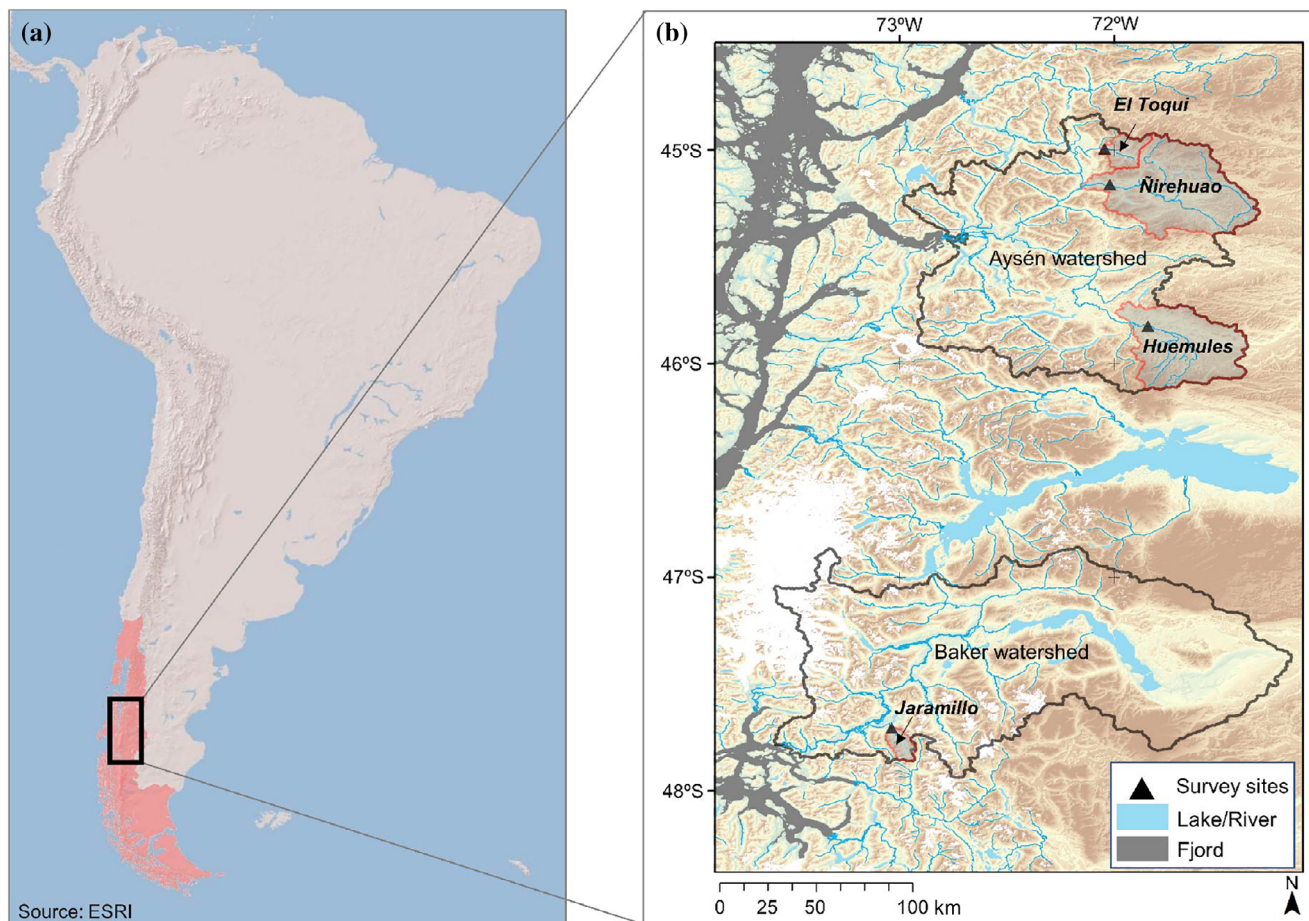
Among the main drivers of global biodiversity loss, invasive species are unique in that their impacts are integrated within biological communities through the creation of novel trophic interactions and the disruption of existing interactions (Jackson et al., 2017). The most severe impacts of invaders are typically due to direct, top-down effects of predation (David et al., 2017; Mollot et al., 2017; Salo et al., 2007). Conversely, non-native species can have positive, bottom-up effects on the species that directly consume them, although any positive effects on the biomass of resident species can be offset by the many indirect effects that can ripple through food webs (e.g., trophic cascades, apparent competition; David et al., 2017; White et al., 2006). The novel interactions that emerge in invaded food webs are influenced by the familiarity of resident species with the invader; that is, their eco-evolutionary experience interacting with the non-native species or with species that are functionally and behaviourally similar to the non-native species (Carthey & Banks, 2014; Pearse & Altermatt, 2013; Saul & Jeschke, 2015). Thus, interactions that an invader has in its native range may re-emerge in invaded food webs if there are resident species that occur in the invader's native range or that are phylogenetically similar to interactors in the invader's native range.

A recent invasion that has been subject to little ecological study despite potentially having significant ecological consequences is that of Chinook salmon (*Oncorhynchus tshawytscha*) in the Patagonia region of southern South America. Chinook salmon were introduced to a few streams in southern Chile in the 1970s and 1980s and have since colonized all of the inhabitable watersheds in southern Chile (39–55°S) as well as Atlantic-draining watersheds in southern Argentina (Figure 1a; Ciancio et al., 2015; Correa & Gross, 2008). Initial research on Patagonian Chinook salmon has largely focused on the origin and life history characteristics of populations (e.g., Araya et al., 2014; Correa & Moran, 2017; Di Prinzio et al., 2015; Musleh et al., 2020). However, little is known about the trophic interactions that have emerged within the food webs invaded by salmon or the consequences of these interactions.

In their native range of Pacific North America and Asia, Pacific salmon (*Oncorhynchus* spp.) have strong interactions with many co-occurring species, largely due to the marine-derived nutrients that they deliver to streams and forests when they spawn and subsequently die. Pacific salmon are anadromous and amass 99% of their body size in the ocean (Quinn, 2005). Their annual return to freshwater to spawn en masse represents a pulse of food for animal consumers as well as a pulse of nutrients for nutrient-limited primary producers (i.e., positive, bottom-up effects). These resources are vital for many consumer taxa. Stream-resident brown trout (*Salmo trutta*) and rainbow trout (*O. mykiss*) feed principally on salmon eggs and carcasses upon the return of adult salmon, with their growth trajectories largely dependent on this consumption (Hermann et al., 2020; Ivan et al., 2011; Scheuerell et al., 2007). Mobile terrestrial consumers such as brown bears (*Ursus arctos*) and glaucous-winged gulls (*Larus glaucescens*) track temporal variation in salmon spawning among watersheds (Field & Reynolds, 2013; Schindler et al., 2013). Adult and juvenile salmon comprise the majority of the diet of riverine American mink (*Neovison vison*) throughout the year (Ben-David et al., 1997), benefitting mink to the extent that the timing of mink lactation has seemingly synchronized with the spawn timing of salmon (Ben-David, 1997).

Such direct effects of salmon on consumer taxa can cause cascading effects through food webs. For example, the abundance of insectivorous birds is positively associated with the abundance of adult salmon among streams (Field & Reynolds, 2011; Wagner & Reynolds, 2019), a relationship explained by aquatic and terrestrial insects being more abundant in salmon-bearing streams (e.g., Verspoor et al., 2011). With such diverse and consequential pathways through which they interact with co-occurring species, Pacific salmon can play a role in the ecological integrity of their native food webs (Darimont et al., 2010; Willson & Halupka, 1995). As such, the potential for Chinook salmon to affect co-occurring species in their non-native range is large.

The aim of this study was to identify species in southern Chile that consume the novel marine-derived resources that adult Chinook salmon deliver to streams



**FIGURE 1** (a) Map of South America showing the regional distribution of Chinook salmon (*Oncorhynchus tshawytscha*) in southern Chile and Argentina (highlighted in red); (b) study streams located throughout the Chilean province of Aysén

and forests, and to conceptualize the potential food web impacts of salmon in Patagonia. Consumption of salmon carcasses in freshwater and riparian habitats was qualitatively monitored using (1) sampling of invertebrate consumers found on submerged and out-of-water carcasses, and (2) motion-activated cameras baited with carcasses to identify vertebrate consumers in the riparian zone. The trophic interactions of Chinook salmon in Patagonia were then summarized using all documented interactions, including those presented here for the first time as well as previously reported observations.

## METHODS

### Study sites

Stream surveys were conducted in the Aysén province of southern Chile (Figure 1). This region is sparsely populated, contains large tracts of temperate rainforest dominated by southern beech trees (*Nothofagus* spp.) intermixed with low-intensity silvopastoral lands, and is

characterized by a strong longitudinal gradient in rainfall that becomes drier towards headwaters in the east. Chinook salmon were first observed in this region in the early 2000s (Correa & Gross, 2008) and have since established annual spawning runs in watersheds throughout the region.

Stream surveys were conducted during the late summer/autumn spawning season (February through June) in 2016 and 2018. In 2016, four streams were surveyed, including three streams in the Río Aysén watershed (El Toqui, Ñirehuao, and Huemules) and one stream in the Río Baker watershed (Jaramillo; Figure 1b). In 2018, the three streams in the Aysén watershed were again surveyed, but Jaramillo was excluded due to logistical constraints. These study systems are third- to fifth-order streams with mean discharges that range from 2.8 to 31.4 m<sup>3</sup>/s (Table 1). During the two studied spawning seasons, each stream was visually surveyed multiple times throughout 1.0–2.3 km of stream reaches. The number of live and dead salmon was opportunistically counted during each survey, and the location of carcasses (in or out of the stream) was also recorded. These counts

**TABLE 1** Stream and survey characteristics for study systems in Patagonia, southern Chile

Stream	Drainage area (km <sup>2</sup> )	Order	Mean discharge (m <sup>3</sup> /s)	Total length (km)	Length of surveys for salmon (km)	Max. live salmon observed <sup>a</sup>	Max. carcasses observed <sup>b</sup>	Carcasses out of water <sup>c</sup> (%)
El Toqui	207	4	4.6	31	1.5	25	17	29
Ñirehuao	1971	5	31.4	65	2.3	26	5	40
Huemules	1423	5	15.8	34	1.8	30	22	32
Jaramillo	117	3	2.8	6	1.0	44	39	36

<sup>a</sup>The maximum number of live adult salmon observed on an individual survey date.

<sup>b</sup>The maximum number of dead adult salmon observed on an individual survey date.

<sup>c</sup>The percent of carcasses found partially or fully out of water on the date that the maximum number of dead salmon was observed.

were not exhaustive given that they were typically conducted from one side of the stream only and spawning salmon and carcasses were observed downstream of the surveyed reaches in every stream. While not representing the total number of salmon in each stream, these counts characterized temporal patterns in spawning behavior and carcass availability.

## Invertebrate consumption

In 2016, invertebrate abundance on Chinook carcasses was quantified during one or two survey dates at all four streams. This survey occurred midway through the spawning season and used naturally occurring carcasses that were encountered while surveying the streams. In total, 39 out-of-water carcasses and 50 underwater carcasses were sampled. Following Chaloner et al. (2002), the relative abundance of invertebrate taxa found on each carcass was estimated as 1–9, 10–99, 100–1000 or >1000 individuals. Larval flies (order: Diptera) on terrestrial carcasses were not identified beyond the order level. Instead, fly larvae were assumed to belong to the adult families that were observed on carcasses throughout the study period in 2016. Submerged carcasses were scanned visually, and invertebrates found on them were removed and stored for later identification (at the order or family level). This aquatic sampling procedure was likely biased against capturing highly mobile consumers such as decapods and did not account for any invertebrates that were inside carcasses. At each stream, taxa were categorized as absent, rare (1–9 individuals), present (10–99), or common (>100) based on their median relative abundance on carcasses.

Given the abundance of terrestrial flies found on carcasses in 2016 (described below), we deployed plastic funnel flytraps baited with salmon carcass flesh midway through the spawning season in 2018 to identify fly consumers at a higher taxonomic level. At El Toqui, Ñirehuao, and Huemules, five traps were left in riparian

habitat for 24 h. Trapped adult flies were identified to the family level, and those belonging to family Calliphoridae (blowflies) were identified to species using González et al. (2017).

In addition to the more formal sampling described above, opportunistic observations of invertebrate interactions with out-of-water carcasses were made throughout both spawning seasons. This included watching individual carcasses to observe invertebrate behavior and photographing individual carcasses on different survey dates to visualize the loss of carcass mass due to invertebrate consumption.

## Vertebrate consumption

Camera traps were used to monitor carcass consumption by terrestrial vertebrates. This monitoring took place at El Toqui, Ñirehuao, and Huemules in 2016 and again at El Toqui and Huemules in 2018. At the onset of carcass availability, one motion-activated camera per stream (Stealth Cam, Grand Prairie, TX) was placed within 10 m of the stream edge and baited with a staked carcass that was found in or along the stream. The carcasses used were spawned-out albeit fresh, being fully intact with few signs of decomposition. Cameras were programmed to take three pictures per trigger, with a 30-s delay between triggers. In 2016, carcasses were monitored for 50, 13, and 45 days at El Toqui, Ñirehuao, and Huemules, respectively. In 2018, they were monitored for 16 and 20 days at El Toqui and Huemules, respectively. At the end of these sampling periods, baited carcasses had either been fully consumed or had only pieces of head, skin, and cartilage remaining. Encounter rates were quantified by counting the total number of camera triggers among consumer taxa at each site and then dividing by the total number of camera-days (i.e., encounters per camera-day). To avoid overestimating encounter rates by including consecutive triggers by the same individual, pictures of the same consumer taxon that were taken consecutively

(i.e., 1 min apart or less) were counted as a single encounter. These data were not analyzed statistically.

During consecutive days of work at El Toqui in March 2018, we observed carcasses that appeared to have been moved from the stream to nearby banks overnight, despite no significant change in water levels. Accordingly, we placed a camera in a cut-bank directly beside the stream edge and placed a carcass in the water in front of the camera. The carcass was wedged underneath a log to keep it submerged and in place. The camera was set to record video and was left overnight.

## Community interactions

We summarized the community interactions involving Chinook salmon in Patagonia by categorizing all documented interactions in freshwater and terrestrial habitats using the framework presented in Simberloff and Von Holle (1999). This framework is used to describe potential food web impacts of invasive species (e.g., Crego et al., 2016) and identifies four types of pairwise species interactions: “+/+” denotes interactions in which individuals of two species directly benefit from the presence of the other species; “+/0” denotes those in which individuals of one species benefit from the presence of the other species, whereas individuals of the second species are not affected by the first (e.g., a donor-controlled subsidy); “+/-” denotes interactions in which individuals of one species benefit from the presence of the other; however, individuals of the other species are negatively affected by the first species (e.g., predator-prey interactions); and “-/-” denotes interactions that are detrimental to individuals from both species. We added “0/+/+” to describe tri-trophic interactions in which individuals from a third species benefit from the presence of the benefitting species in a “0/+” interaction. These categories describe individual-level interactions. These interactions could have population-level consequences for one or both species and therefore conceptualize potential food web impacts of invaders. The salmon interactions used here include those described in this study as well as those previously reported in the literature. Published observations were obtained by searching Web of Science using the search term “(Chinook salmon AND (“Chile” OR “Argentina” OR “Patagonia”)).”

If Chinook and an interacting taxon have multiple interaction types in another location (e.g., the native range of salmon), all of these interaction types were inferred to be present in Patagonia if at least one of the interactions was documented in Patagonia. Indirect interactions involving Chinook (e.g., tri-trophic interactions 0/+/+) were only included if they were directly observed.

Likewise, negative interactions resulting from exploitative competition (-/-) were only included if shared prey items have been shown to be limiting. Aquatic macroinvertebrates and terrestrial insects were considered two groups of interacting organisms, with interactions with individual taxa beyond the scope of this analysis. Interactions among the interacting taxa (i.e., not involving Chinook salmon) were not assessed.

## RESULTS

### Carcass availability

Across streams in both 2016 and 2018, adult Chinook salmon occupied pool habitats in mid-February and then occupied riffle-run transition habitats throughout March and April and displayed breeding behaviors such as redd construction and maintenance. Carcasses appeared between early March and early April (depending on the stream) and were observed on final survey dates in early June, weeks after spawning had completed. Few carcasses were observed at Ñirehuao relative to the other streams (Table 1). On the day that the maximum number of carcasses was observed at each stream, 29%–40% of carcasses were found partially or fully out of water (Table 1).

### Invertebrate consumers

In 2016, the adult flies found eating or laying eggs on out-of-water carcasses were primarily blowflies (family: Calliphoridae) (Figure 2a) but also included flesh flies (Sarcophagidae) and March flies (Bibionidae) (Appendix S1: Figure S1). Terrestrial flies were abundant on carcasses, averaging over 1000 larvae per carcass across all streams (Table 2). Larvae were typically found on the underside of carcasses (Figure 2b), on gills, in the mouth, and under fins (Figure 2c). Heavy colonization of carcasses by fly larvae caused rapid depletion of carcass mass, with individual carcasses changing from nearly whole to only skin, cartilage, and bones within a few days (Figure 2c,d). Flytraps (baited with carcass flesh) were successful in attracting flies, with each trap typically containing well over 100 individuals. Blowflies comprised over 95% of the trapped flies at each stream. Of the blowflies, 99% of individuals were the cosmopolitan species *Calliphora vicina*. Flesh flies were also found in the traps (<5% of trapped flies).

Non-native yellow jacket wasps (genus *Vespula*) were found on several out-of-water carcasses at Ñirehuao and Jaramillo (Table 2; Appendix S1: Figure S1d). There were



**FIGURE 2** Colonization and consumption of out-of-water salmon carcasses by terrestrial flies in southern Chile. Pictured are (a) adult blowflies (*Calliphoridae*) on a fresh carcass, (b) hundreds of fly larvae on the underside of a carcass, (c) fly larvae under a carcass fin, and (d) a carcass left with only skin, cartilage, and bone after fly consumption. Photos (c) and (d) show the same carcass 6 days apart, illustrating rapid loss of carcass mass due to fly consumption

**TABLE 2** Median abundance of terrestrial and aquatic invertebrate taxa found on naturally occurring Chinook salmon carcasses at four streams in southern Chile

Taxon	Stream			
	Ñirehuao	El Toqui	Huemules	Jaramillo
Terrestrial				
Diptera <sup>a</sup>	+++	+++	+++	+++
Hymenoptera				
Vespidae	+	–	–	+
Aquatic				
Diptera				
Chironomidae	++	++	++	++
Simuliidae	+	+	–	++
Plecoptera	+	+	+	+
Trichoptera	+	+	–	–

*Note:* Terrestrial taxa colonized carcasses that were out of water, whereas aquatic taxa colonized submerged carcasses. Abundance categories are – (absent), + (rare; 1–9 individuals), ++ (present; 10–99 individuals), and +++ (common; >100 individuals).

<sup>a</sup>*Calliphoridae*, *Sarcophagidae*, and *Bibionidae*.



**FIGURE 3** Evidence of vertebrate consumption of (a) a partially submerged carcass in Río El Toqui, and (b) a carcass in riparian habitat at Río Huemules. Such carcasses were found largely consumed with mostly bones remaining, indicating consumption by animal scavengers



**FIGURE 4** Chinook salmon carcass visits by (a) a small rodent, (b) a chucao, (c) an American mink, and (d) a culpeo fox. Carcasses were staked in riparian habitat adjacent to streams in southern Chile

also several opportunistic observations made in 2018: dozens of carrion beetles from the family Silphidae (genera *Oxelytrum* and *Nicrophorus*) were observed feeding

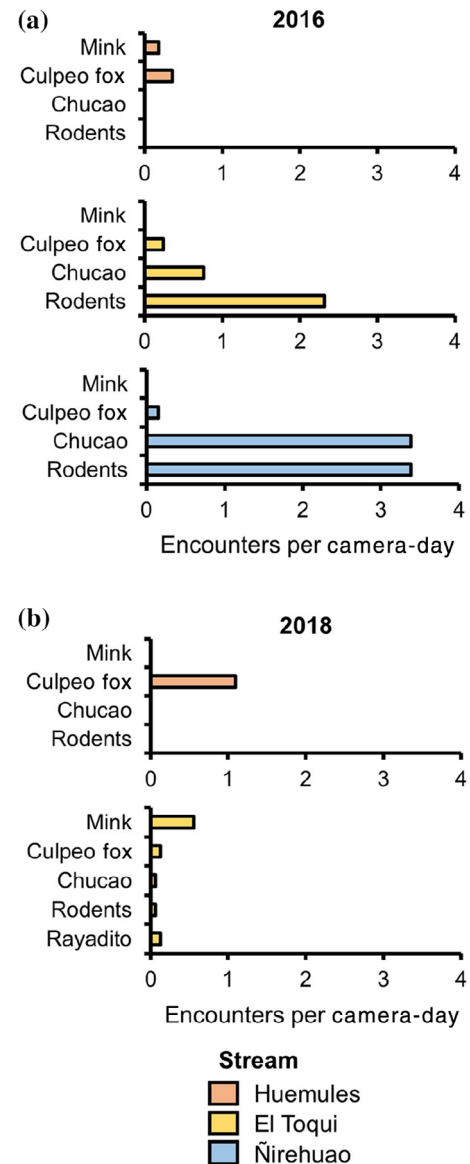
on multiple carcasses (Appendix S1: Figure S2); predatory beetles (Staphylinidae and Carabidae: *Ceroglossus*) fed on insects that were feeding on a carcass; predatory balloon

flies (Empididae: Hemerodromiinae) hunted small Acaliptratae flies that were feeding on a carcass; and, lastly, a male Darwin's beetle (*Chiasognathus grantii*) was observed feeding on carcass liquids and fending off other males from a carcass.

Carcasses submerged underwater had lower levels of invertebrate abundance relative to riparian carcasses (Table 2). Chironomid midge (Chironomidae) larvae averaged 10–99 individuals per carcass at all four streams. Blackfly (Simuliidae) larvae were the second most abundant taxon, although they were likely not feeding directly on carcasses because they attach themselves to substrate and feed on floating organic debris. Stoneflies (Plecoptera) and caddisflies (Trichoptera) were rare (i.e., 1–9 individuals per carcass on average), while mayflies (Ephemeroptera) were found on several carcasses but were absent from carcasses on average. Weeks after the appearance of carcasses (late April and May), underwater carcasses were covered with a thick, mold-like biofilm (Appendix S1: Figure S3).

## Vertebrate consumers

Evidence of vertebrate consumption of naturally occurring carcasses was commonly observed during surveys (Figure 3). Camera trap monitoring in 2016 found four vertebrate taxa that consumed riparian carcasses: small rodents (black rats *Rattus rattus*, house mice *Mus musculus*, and/or colilargos *Oligoryzomys longicaudatus*), the ground-foraging passerine bird “chucaos” (*Scelorchilis rubecula*), the South American fox “culpeo” (*Lycalopex culpaeus*), and the invasive American mink (Figure 4). Encounter rates varied among species and streams (Figure 5a). At Ñirehuao and El Toqui, rodents and chucaos averaged multiple encounters per camera-day whereas foxes were less common; conversely, only foxes and mink were encountered at Huemules (Figure 5a). Foraging behavior was not directly evident in some encounters; however, foraging on carcasses was frequently observed for each consumer taxa. Rodents foraged extensively adjacent to and directly on carcasses, and only at night. Species identification for these rodent encounters was challenging due to their nocturnal activity and their morphological similarity. Although definitively identifying species was not possible, there were visual indications for the native cricetid “colilargo” as well as the non-native black rat and house mouse, suggesting that the encounters consisted of a combination of these three species. Chucaos visited carcasses during daylight and demonstrated gleaning behavior, feeding on invertebrates that had colonized the carcasses. Foxes visited carcasses both day and night, often urinated



**FIGURE 5** Vertebrate consumers of out-of-water salmon carcasses in southern Chile. Camera traps were baited with salmon carcasses adjacent to streams. Consumer encounter rates per camera-day were calculated (a) for three streams in 2016 and (b) for two streams in 2018. Consumer taxa were American mink, culpeo fox, a passerine bird “chucao,” rodents (black rats, house mice, and/or colilargos), and a passerine bird “thorn-tailed rayadito”

on carcasses seemingly without feeding on them, and occasionally ripped off large portions of the carcass when feeding. Mink were only encountered at nighttime and were observed biting at the carcass and attempting to remove it. Mink encounters occurred within a week of the camera trap being set, likely indicative of a preference for fresh prey.

During camera trap monitoring in 2018, culpeo foxes averaged over one carcass encounter per day at Huemules and were again present at El Toqui



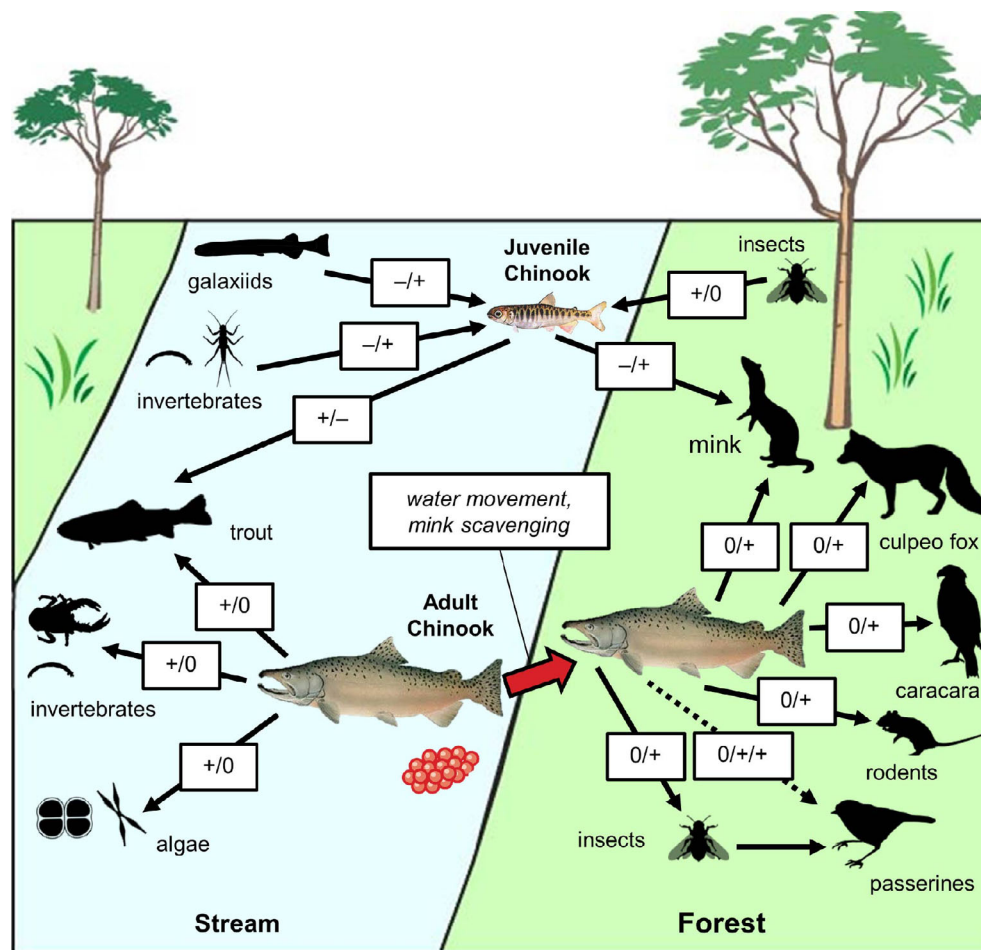
(Figure 5b). Mink were not encountered at Huemules but were encountered at El Toqui and, again, these encounters only occurred within 1 week of the camera trap being set. Rodents and chucaos were encountered less frequently at El Toqui in 2018 compared to 2016 (Figure 5). Additionally, the passerine bird “thorn-tailed rayadito” (*Aphrastura spinicauda*) visited the carcass at El Toqui and seemingly fed on invertebrates off the carcass. Across streams and years ( $n = 5$ ), lower rates of fox and mink encounters (combined) were associated with increased rates of rodent and passerine encounters (Appendix S1: Figure S4).

Video monitoring of a submerged carcass in El Toqui showed an individual mink walking along the streambank, submerging its head repeatedly to feed on

the carcass, making repeated attempts to dislodge the carcass, and, finally, feeding on the carcass along the streambank after having removed it from the water (Appendix S1: Figure S5; Video S1). This footage demonstrates carcass transfer from stream to streambank by a vertebrate scavenger.

## Community interactions

The literature search yielded 65 returns, of which 6 contained observations of trophic interactions between Chinook salmon and freshwater or riparian taxa (Appendix S2: Table S1). Including those presented here, the documented interactions in Patagonia consist of



**FIGURE 6** Trophic interactions involving Chinook salmon in streams and forests of Patagonia. All documented interactions were classified following Simberloff and Von Holle (1999): “+/0” denotes interactions in which individuals of one species benefit whereas individuals of the other species are not affected; “+/-” denotes interactions in which individuals of one species benefit whereas individuals of the other species are negatively affected; and “0/+/+” denotes a tri-trophic interaction whereby individuals from a third species benefit from the presence of the benefitting species in a “0/+” interaction. For terrestrial interactions, salmon correspond with the first taxon in each interaction (e.g., “0” in “0/+”), whereas they correspond with the second taxon in each freshwater interaction. *Black arrows* represent direct interactions, the *dashed arrow* represents an indirect interaction, and the *red arrow* represents the transfer of carcasses from streams to riparian habitat

scavenging salmon carcasses or spilt eggs (0/+,  $n = 7$ ), predator–prey interactions (−/+ or +/−,  $n = 4$ ), nutrient subsidies (0/+,  $n = 1$ ), terrestrial prey subsidies (+/0,  $n = 1$ ), and tri-trophic interactions (0/+/,  $n = 1$ ; Appendix S2: Table S1). Other than a nutrient subsidy effect on stream algae (Muñoz et al., 2021), none of these interactions have been studied at the population level (i.e., impacts on abundance or biomass).

Our proposed framework of the role of Chinook salmon in Patagonian food webs reveals numerous interactions involving a diverse group of taxa and trophic levels (Figure 6). In streams, nutrients from adult salmon carcasses benefit stream algae (Muñoz et al., 2021), and salmon carcasses or spilt eggs are scavenged by trout and macroinvertebrates such as chironomid midges and freshwater crabs (*Aegla* sp.; Arismendi & Soto, 2012; Soto et al., 2007). As predators, juvenile or subadult salmon negatively affect native galaxiid fishes (family: Galaxiidae) and macroinvertebrates such as mayfly and stonefly nymphs (Bravo et al., 2019; Chalde & Fernández, 2017; Di Prinzio & Arismendi, 2018; Ibarra et al., 2011). As prey, juvenile salmon likely benefit adult trout and riverine mink (Ben-David et al., 1997; Tabor et al., 2004). Terrestrial insects that fall into streams benefit juvenile salmon as a donor-controlled prey resource (Chalde & Fernández, 2017; Di Prinzio & Arismendi, 2018). Adult salmon carcasses are transferred to terrestrial habitat by water movement and mink scavenging. There, carcasses are heavily consumed by terrestrial insects such as blowflies, which are in turn consumed by passerine birds such as the chucao and rayadito. Out-of-water carcasses are also scavenged by birds of prey (chimango caracara [*Milvago chimango*] and southern crested caracara [*Caracara plancus*]; Soto et al., 2007), culpeo foxes, and small rodents, including non-native house mice and black rats. The only taxa with multiple beneficial interactions are non-native trout and mink. The only taxon with a net negative interaction with Chinook is galaxiid fishes.

## DISCUSSION

The observations presented in this study reveal a multitude of trophic interactions involving Chinook salmon in Patagonia, including the re-emergence of historical interactions from the native range of Pacific salmon. These interactions have emerged rapidly, with Chinook salmon being first reported in our study streams in the early 2000s (Correa & Gross, 2008). The diverse taxa and trophic levels that interact with Chinook salmon in Patagonia suggest a potential for diverse impacts of salmon on Patagonian food webs.

The postspawn fate of anadromous fish carcasses is mediated by a suite of physical and biological factors such as hydrology, hydromorphology, predation, and scavenging (Dunkle et al., 2020; Harding et al., 2019). For example, Pacific lamprey (*Entosphenus tridentatus*) carcasses are retained instream in depositional microhabitats whereas they are washed out onto riparian habitat alongside high-velocity stream segments (Dunkle et al., 2020), and predation by bears and wolves can transfer up to 23% of spawning Pacific salmon in a stream to the riparian zone (Harding et al., 2019). Here, the ratio of dead to live Chinook salmon observed was 68%–89% at El Toqui, Huemules, and Jaramillo and only 19% at Ñirehuao. The relatively low number of carcasses found at Ñirehuao could be driven by the exceptionally high flows of water in this stream (mean discharge = 31.4 m<sup>3</sup>/s), which can flush carcasses downstream (Richey et al., 1975). We also found that 29%–40% of carcasses were deposited out of water. Whereas the lack of bears and wolves in Patagonia should limit the number of salmon carcasses that are biologically transferred to riparian habitat, we show here that non-native mink can actively remove carcasses from streams via scavenging, and the same is likely true for other large scavengers such as foxes, dogs, and vultures. This active transport of carcasses should increase the degree to which marine-derived nutrients enter terrestrial food webs in Patagonia.

The novel interactions that emerge in invaded food webs can be predicted in part by the phylogenetic similarities between species in the invaded food web and species from the food web that the invader is native to (Pearse & Altermatt, 2013). This influence of eco-evolutionary experience suggests that interactions from the native range of an invader may functionally re-emerge in invaded food webs via resident species that are closely related to interactors in the invader's native range. In Patagonia, we found that many species consume the nutrients provided by postreproductive salmon and that these positive effects extend to a variety of native taxa such as blowflies, beetles, passerine chucaos, culpeo foxes, and chironomids. All of these taxa are closely related to species in North America that similarly derive benefits from salmon consumption. For example, North American blowflies are a dominant vector of salmon nutrients in terrestrial food webs, colonizing over 90% of carcasses (Hocking & Reimchen, 2006) and numbering up to 50,000 larvae on individual carcasses (Meehan et al., 2005). Blowflies increase in abundance due to salmon consumption so much so that they have induced a phenological link between salmon spawning and the flowering of a plant (*Angelica genuflexa*) that blowflies pollinate as adults in Alaska (Lisi & Schindler, 2011). Among streams in British Columbia, the abundance, nest density, and territory

size of Pacific wrens (*Troglodytes pacificus*)—insectivorous passerines similar to chucaos—are positively associated with the abundance of spawning salmon (Wagner & Reynolds, 2019; Wilcox et al., 2021). Like culpeo foxes in Patagonia, coyotes (*Canis latrans*) scavenge salmon carcasses in Alaska (Levi et al., 2015). Submerged salmon carcasses in Alaska are most heavily colonized by chironomid midge larvae (Chaloner et al., 2002), as was found here. These results indicate that many of the pathways of salmon nutrient incorporation in North American food webs have functionally re-emerged in South America via phylogenetically similar native species, supporting the hypothesis that eco-evolutionary history mediates the interactions and impacts that stem from biological invasions (Carthey & Banks, 2014; Pearse & Altermatt, 2013; Saul & Jeschke, 2015).

Most interactions among co-occurring non-native species are either neutral or antagonistic (Jackson, 2015); however, many facilitative interactions have been documented and have raised concerns over their potential to increase the community-level impacts of invasive species (i.e., “invasional meltdowns”; Simberloff & Von Holle, 1999; Simberloff, 2006). A mechanism that could promote this facilitation is an evolutionary history of coexistence (Arismendi et al., 2020; Best & Arcese, 2009). Rainbow trout and mink coexist with Pacific salmon in their native range. There, they strongly benefit from the annual pulse of salmon eggs and carcasses (Ben-David, 1997; Scheuerell et al., 2007) and also prey on juvenile salmon (Ben-David et al., 1997; Tabor et al., 2004). Similarly, brown trout coexist with Atlantic salmon in their native range and strongly benefit from the consumption of Chinook salmon eggs in tributaries of the Laurentian Great Lakes (Hermann et al., 2020), where they are both introduced. In Patagonia, rainbow trout and brown trout consume salmon eggs and mink scavenge salmon carcasses during salmon spawning. The eco-evolutionary experience that trout and mink have with salmon likely means that they are preadapted for such consumption and could consequently be key beneficiaries of the salmon invasion of Patagonia. Trout and mink are now widespread in Patagonia and negatively affect the abundance and distribution of many native species (Arismendi et al., 2012; Correa & Hendry, 2012; Habit et al., 2010; Schüttler et al., 2009; Valenzuela et al., 2013). Other invasive species that benefit from salmon consumption in Patagonia include yellow jacket wasps, house mice, and black rats. It has also been speculated that Chinook in Chile might act as a vector for the invasive diatom *Didymosphenia geminata* (Bus Leone et al., 2014), though this remains untested. These observations add to the growing number of interactions among non-native species in Patagonia (Crego et al., 2016). As

these interactions increase in strength and complexity, non-native species will continue to alter these otherwise minimally impacted ecosystems.

The native aquatic fauna of Patagonia is characterized by low species richness and high levels of endemism, and many of the galaxiid fishes that dominate the native freshwater fish assemblage are imperiled (Habit & Cussac, 2016). The interactions framework proposed here suggests that galaxiids are likely the “loser” of the Chinook salmon invasion of Patagonia given that they are the only taxon with a net negative interaction with Chinook. Furthermore, galaxiids are likely to have an indirect negative interaction with salmon due to the positive effects of salmon on trout and mink, both of which are galaxiid predators (Arismendi et al., 2012; Valenzuela et al., 2013). On the other hand, galaxiids and other native fishes might benefit from the consumption of salmon eggs and tissue; however, such consumption is likely limited because trout competitively exclude other stream fishes from salmon resources (Bailey & Moore, 2020). Throughout the southern hemisphere, galaxiids have declined as a result of salmonid introductions (Habit et al., 2010; Lintermans et al., 2020; Shelton et al., 2015; Townsend, 2003). Given that the potential for coexistence appears to be low, the protection of salmonid-free, hydrologically isolated habitat should be an urgent priority for conservation efforts in Chile.

The interactions framework presented here provides the first assessment of the pathways through which Chinook salmon can impact terrestrial and freshwater food webs in Patagonia. All of the interacting taxa occur throughout much of the South American range of Chinook salmon, meaning the observed interactions likely take place across a large spatial scale. The list of interactors is certainly incomplete due to the limited scope of our field surveys. Other types of interactions that have not yet been studied include responses to salmon-derived nutrients among riparian plants (e.g., Hocking & Reynolds, 2011; Siemens et al., 2020), consumption of juvenile salmon and salmon eggs by forest birds (e.g., Tonra et al., 2016), the transport of salmon-derived nutrients into terrestrial food webs through the emergence of stream insects (e.g., Francis et al., 2006), microbial interactions (discussed below), and bioturbation effects due to disturbance of the streambed (e.g., Moore & Schindler, 2008). Moreover, the prevalence of these interactions likely varies spatially and temporally due to variation in physical and biological characteristics of ecosystems. For example, salmon-derived nutrients increased algal biomass in Ríos El Toqui, Huemules, and Jaramillo, whereas there was no such subsidy effect detected in Ñirehuao, the study stream with the greatest discharge (Muñoz et al., 2021). Despite these caveats, this interactions framework can help guide future

research on population- and community-level impacts of non-native salmon in streams and forests.

Whereas our interactions framework focuses on macroorganisms, interactions with microorganisms could be similarly consequential. In the native range of salmon, the internal microbiome of aquatic mayflies and terrestrial blowflies is influenced by the presence of salmon and the microbial assemblage associated with salmon carcasses (Pechal & Benbow, 2016). Thus, as salmon create a novel link between marine and freshwater habitats in Patagonia, a novel assemblage of microbes might be incorporated by direct and indirect consumers of salmon. Future studies should expand on our interactions framework such that the microbial ecology of this invasion is better understood (e.g., Irgang et al., 2019).

The ecological consequences of these interactions will largely depend on how abundant salmon become in Patagonia. Monitoring of the abundance of Chinook salmon in Patagonia has been rare but will presumably grow given the emerging artisanal fishery for Chinook salmon in the coastal waters of southern Chile. An assessment of spawning numbers in the Río Toltén watershed in Chile estimated that over 12,000 adult Chinook returned to this watershed between 2014 and 2015 (Gomez-Uchida, 2014). These numbers are comparable to Chinook populations in British Columbia, where the annual spawner abundance in individual populations generally does not exceed a few tens of thousands (Gottesfeld et al., 2008) and is often less than 1000 (Healey, 1982). Without the other, more abundant species of Pacific salmon, the effects of salmon in Patagonia will be less pervasive than in North America. Nevertheless, the freshwater ecosystems of southern South America are some of the most nutrient-limited systems in the world (Dentener et al., 2006; Perakis & Hedin, 2002), meaning the novel inputs of marine-derived nutrients should be highly utilized by plants and animals (Sears et al., 2004). Moreover, recent evidence indicates that coho salmon (*O. kisutch*) have established self-sustaining populations in southern Chile (C. Correa, personal observations; Górski et al., 2016; Maldonado-Márquez et al., 2020), suggesting that the abundance of Pacific salmon will continue to increase in the region. Going forward, expanded monitoring of the abundance and impacts of Patagonian salmon will be vital if managers are to balance the socioeconomic benefits with the ecological costs of this invasion.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data (Muñoz, 2021) are available from Figshare: <https://doi.org/10.6084/m9.figshare.c.5702668.v1>.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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