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Review

Historical and Contemporary Diversity of Galaxiids in South America: Biogeographic and Phylogenetic Perspectives

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Abstract: Galaxiid fishes from South America are represented by three genera (*Aplochiton*, *Brachygalaxias* and *Galaxias*) and eight species. Their genetic patterns have been studied over the last two decades to disentangle how historical and contemporary processes influenced their biogeographic distribution and phylogeographic patterns. Here we review and synthesize this body of work. Phylogeographic approaches reveal the important role played by orogeny and the expansion/melting of glacial ice during the Quaternary. Populations retreated to glacial refugia during glacial times and some systems experienced drainage reversals from the Atlantic to the Pacific following deglaciation. Although most species expanded their populations and increased their genetic diversity during the Holocene, the introduction of salmonids and the construction of dams are likely to lead to a decline in genetic diversity for at least some species. An improvement in our understanding of the processes that influenced historical and contemporary diversity patterns among galaxiid and other native fishes in South America is necessary for addressing the cumulative and synergistic impacts of human activity on this unique freshwater fauna.

Keywords: Galaxiidae; fish; Patagonia; genetics; phylogeny

1. Introduction

Galaxiid fishes (Galaxiidae) in South America are represented by three genera and eight species (*Galaxias maculatus*, *G. platei*, *G. globiceps*, *Aplochiton zebra*, *A. marinus*, *A. taeniatus*, *Brachygalaxias bullocki*, *and B. gothei*) distributed throughout the Southern Cone in continental Patagonia on both sides of the Andes as well as in Tierra del Fuego and the Falkland/Malvinas islands ([1]; Figure 1A). The various species in the group differ in their life histories, and though their respective ranges overlap, they differ substantially in their distributions. *Galaxias maculatus* and *G. platei* are the two most widespread species in the group and their distributions coincide with the area covered by the icecap during the Last Glacial Maximum (LGM), including the area west of the icecap north of Lat 42° S where the ice coverage did not reach the sea (Figure 1B). One difference between these two species, however, is that *G. maculatus* (but not *G. platei*) is present in estuarine and coastal areas as indicated below. The other species in the group are also found within the area covered by the LGM icecap, but they tend to be present less frequently and in smaller numbers than *G. maculatus* [2].

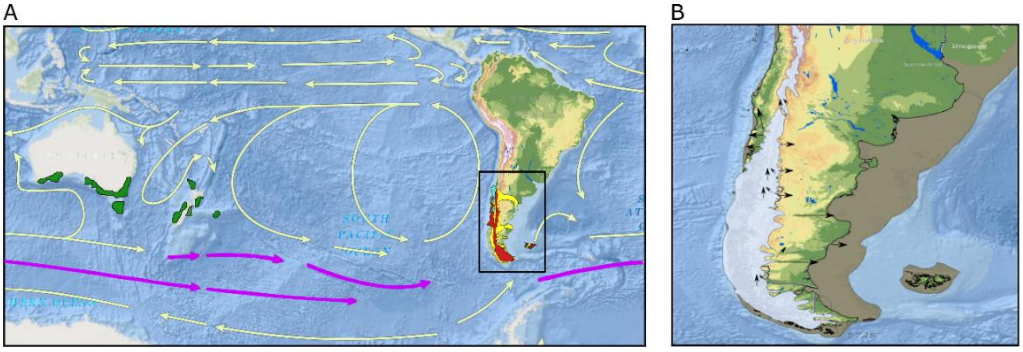

Figure 1. (**A**) Southern hemisphere map including *Galaxias* (in yellow), *Aplochiton* (in red), and *Brachygalaxias* (in light blue) range species from South America and *G. maculatus* range outside of South America (in green). West Wind Drift in magenta arrows. (**B**) South America zoomed map with schematic main landscape changes in Patagonia and presumed direction of retreat to glacial refugia (marked with arrows) explaining the principal phylogeographic patterns of galaxiid species during glacial times. Approximate glacial ice cover at the time of the Last Glacial Maximum (LGM) shown in grey. Exposed area of Patagonia during the LGM (in dark grey) due to sea level drop (180 m) (See [3,4]). Paleocoast during the Last Glacial Maximum based on free data available from https://crc806db.uni-koeln.de/layer/show/327/.

Galaxias maculatus, the most widely distributed species in the group exhibits both freshwater resident (whether landlocked or not) as well as diadromous populations. Diadromous populations inhabit estuarine and coastal marine habitats along the Pacific coast [5], the Atlantic coast in southernmost Patagonia [6] as well as the island of Tierra del Fuego [7]. *Galaxias maculatus* has a relatively short generation time; individuals usually reach maturity before their first year of life, with the most common cohort among reproductively mature individuals often being the 1+ cohort. Adults > 3 years of age are rarely found [8]. Freshwater resident *G. maculatus* lay their eggs in littoral zones of lakes and on riverine floodplains with abundant vegetation, exhibiting a repetitive spawning strategy [8–10]. After hatching, larvae undertake significant habitat shifts, migrating from the littoral to the limnetic zone [11]. In estuaries, *G. maculatus* spawns on the top of flooded grass flats after the highest high-water spring tide [12]. As the tide recedes, the eggs are washed down to the bases of the grass clumps where the high humidity of the vegetation protects them from desiccation until the next spring tides a fortnight later [13]. Larvae are subsequently washed out to sea where the juveniles spend approximately six months before returning to freshwater. Hatching during flood events may favor larval survival as turbid flows likely provide cover as larvae migrate out to sea [14]. *Galaxias maculatus* form large shoals that swim during the day; they tend to feed on zooplankton in lakes and benthic macroinvertebrates in rivers, floodplains, and estuaries. Lacustrine individuals tend to have a more fusiform body, narrower heads, and larger eyes than riverine individuals [15]. Similar morphological divergence patterns have recently been described for other galaxiid species inhabiting lentic and lotic environments [16].

Galaxias platei, a strictly freshwater species largely restricted to lacustrine environments, is distributed throughout Andean Patagonia and Tierra del Fuego. Their juveniles are most commonly found in the shallow littoral zone of lakes, while large adult individuals inhabiting multispecies communities are most common in deep benthic areas below the thermocline and euphotic zones, presumably to avoid predation by other natives (e.g., *Percichthys trucha*) or introduced salmonid species [17–19]. When present in single species lakes, *G. platei* can be found throughout the pelagic and benthic environments [20]. *Galaxias platei* can live up to approximately 20 years [20]. Authors have reported lengths at 50% maturity for females and males inhabiting a northern Patagonian lake to be 10.5 cm and 17.7 cm, respectively [21]. These sizes likely correspond to ages 2–4 but age at 50% maturity likely varies with biotic (i.e., presence of predators) and abiotic (e.g., latitude) variables. A recent study examining the potential consequences for *G. platei* of habitat fragmentation by hydroelectric dams assumed generation time for this species to be around 3.5 years [22] but further research to assess the degree to which age at 50% maturity, age-specific survival and fecundity rates, adult life span and other life history traits vary with biotic and abiotic factors is needed.

The species exhibits a fusiform body shape influenced by predation intensity: individuals in high predation environments have relatively short tails presumed to be relevant for burst swimming [18,19]. It also shows some physiological characteristics that enable it to live in the deep and cold water in glacial fed lakes, including a broad thermal tolerance range [21,23]. The species preys on fish, crustaceans, insects, mollusks, and annelids [19] and exhibits cannibalism in single species lakes [24].

Galaxias globiceps, *Brachygalaxias bullocki*, and *B. gothei* are strictly freshwater fish and are generally present in low numbers [2]; their life histories are largely unknown. *Galaxias globiceps* is restricted to small streams near Puerto Montt (Lat. 41.47° S) and the Chiloé Island in Chile [25,26]. *Brachygalaxias bullocki* is found in river systems from the Maule river basin (Lat. 35° S) to Chiloé Island. It typically inhabits streams and rivers with high levels of humic acids, lowland rivers with native riparian forest, large floodplains, and forested wetlands [2,27]. *Brachygalaxias gothei* is restricted to small ditches in central Chile (Lat. 32–38° S) [28].

The remaining three galaxiid species in Patagonia, all Aplochitonidae, are represented by one catadromous (*A. marinus*), one facultative catadromous (*A. taeniatus*), and a strictly freshwater species (*A. zebra*) [29]; they can be found coexisting in the Valdivia (Lat. 39° S) and Maullín (Lat. 41° S) river systems as well as on Chiloé Island [2]. *Aplochiton zebra* and *A. taeniatus*, though widely distributed from central Chile to Tierra del Fuego and the Falkland (Malvinas) Islands, appear less frequently and in lower numbers than the *Galaxias* species in the same areas [2,30,31]. *Aplochiton marinus* is distributed from the Valdivia (Lat. 39° S) to the Aysén (Lat. 45° S) river systems, associated with estuarine habitats [29,32]. Species in the genus *Aplochiton* use shallow rapids or riffles in rivers as juveniles and move to lakes or deep river pools as adults [2]. These species feed on benthic macroinvertebrates and winged Diptera jumping out of the water. This feeding behavior is suppressed in the presence of salmonids [33].

Although several ecological and biogeographic studies exist that focus on South American galaxiid fishes, only 24 studies (using allozymes, DNA sequences, microsatellites, and Single Nucleotide Polymorphic markers (SNPs)) have thus far addressed questions concerning their phylogeographic and landscape genetic patterns (Table 1), but no study has yet synthesized their main results. Collectively, these studies have made significant progress towards elucidating the processes that influenced their current distribution in the region. The two long-term processes claimed to have had a major influence on phylogeographic patterns in this region of the world include the uplift of the Andes and the glacial cycles of the Quaternary [34–36]. Over more recent and shorter time scales, though, human impact, via the introduction of invasive species and the construction of dams for hydropower generation, has also affected species distributions [2,37] and genetic diversity [38,39].

Table 1. Genetic markers (DNA sequences, microsatellites, and Single Nucleotide Polymorphic markers (SNPs)) for South American galaxiid fishes and publications where they were analyzed.

Genus	Species	DNA Sequences	Microsatellites	SNPs
Galaxias	*maculatus*	[35,36,40–48]	[6,43,49]	[5]
	platei	[34,36,42,47,48,50,51]	[22,38,39]	
	globiceps	-	-	-
Aplochiton	*taeniatus*	[32,43,47,52]	[32,52]	
	zebra	[32,41,43,47,52]	[32,52]	
	marinus	[32]	[32]	
Brachygalaxias	*bullocki*	[42]		
	gothei	[42]		

A variety of approaches have been used to examine phylogeographic and landscape genetic patterns in galaxiid fishes in Patagonia and they have all contributed to our understanding of the processes that affected the biogeography and current distribution of these fish species in the region and indeed to our understanding of how they are likely to respond to future potential changes in climate. Phylogenetic studies based on DNA sequences (e.g., mtDNA and nDNA) can give insights on the long-term processes, which for galaxiids include processes such as the fragmentation of Gondwana and the appearance of mountain chains as a barrier for species dispersal [41,42]. DNA sequences have also been used to study phylogeographic patterns over shorter time scales in galaxiids (e.g., [34–36,47,48,50,53]). The information obtained using mtDNA sequences has more recently been complemented with studies based on nuclear microsatellite markers (e.g., [32,38,43]) and Single Nucleotide Polymorphisms (SNPs, [5]), which tend to focus on processes that take place over relatively short historical and contemporary time scales (thousands of years to a few generations ago).

Below, we summarize the phylogeographic and landscape genetic information available for Galaxiidae in Patagonia. We focus on what we have learned from these studies and discuss some of their possible pitfalls.

2. Phylogenetic Relationship of South American Galaxiids

Two studies have generated the most exhaustive phylogenetic studies on galaxiid species worldwide [41,42]. These studies included DNA sequences of six of the eight galaxiid species found in South America (*Galaxias globiceps* and *Aplochiton marinus* were not included in the analyses) and they revealed that the South American species fall into five groups with *Aplochiton spp*. being the most differentiated group, followed by *Brachygalaxias* and *G. maculatus*. They also provided evidence suggesting that *G. platei* is perhaps the most puzzling South American species, forming part of a clade conformed by species in the genus *Neochanna*. The phylogenetic position of *G. platei* observed by these authors [42] using DNA sequences, separated from its closely distributed congeneric species *G. maculatus*, has also been observed in a more recent study [51] using the complete mitogenome of *G. platei*. The phylogeny of Galaxiids and estimated divergence times [42] have suggested that the distribution of galaxiid fishes was potentially explained by Gondwanan vicariance preceded by marine dispersal with the separation of the *Aplochiton-Lovettia* clade from all other galaxiid species in the Cretaceus (circa. 70 Mya) with the *Aplochiton-Lovettia* divergence taking place subsequently during the Paleocene (circa 55 Mya). This divergence time reveals that *Aplochiton spp*. are the oldest galaxiid species in South America. This divergent event is followed by the appearance of *Brachygalaxias* spp. during the Eocene (circa 46 Mya). *Galaxias platei* then diverged from *Neochanna* during the Oligocene (circa 31 Mya), and *G. maculatus* diverged from *G. rostratus* during the Miocene (circa 7 Mya). Further research encompassing other species not yet examined including *Galaxias globiceps* and *Aplochiton marinus* is needed to improve our understanding of the phylogenetic relationship and divergence times among the galaxiid species in South America. Ideally, this should include a complete phylogenetic reconstruction based on whole genome sequencing.

3. Phylogeography and Landscape Genetics Studies on Galaxiid Fishes

The Andean uplift (90–15 Myr BP), the Quaternary glaciations (2.58 Myr BP to 10,000 BP) and the sea level rise during the Holocene (11,700 BP to present day) have all had a profound influence on the contemporary geography of South America and consequently, on contemporary genetic patterns for both aquatic and terrestrial species inhabiting the region [54,55]. For instance, the glacial periods of the Quaternary [56], when plants and terrestrial vertebrates [57] as well as freshwater fishes retreated to glacial refugia and migrated to unglaciated areas, can be traced with genetic markers (Figure 1). These past landscape changes affected galaxiid fishes differently in different areas, depending not just on life histories but also their proximity to glaciers, distance to the coastline, and available ice-free continental area. Phylogeographic patterns have thus far been examined for only five of the eight galaxiid species in South America. No information exists yet on the phylogeography of the two *Brachygalaxias* species, nor for that of *Galaxias globiceps*, in part likely because of their relatively limited geographic range. Below, we synthesize the available information.

3.1. *Galaxias maculatus*

Galaxias maculatus is the most widely distributed galaxiid and the most intensely studied member of the family at the genetic level in South America. The species has a Gondwanan distribution and can thus be found in South America, Australia, and New Zealand [12,58]. Earlier studies on the phylogeographic patterns of *G. maculatus* using DNA sequences found that South American populations are classified into a single group well differentiated from the Tasmania–New Zealand populations [42]. Estimates of divergence time derived under a molecular clock assumption suggest the *G. maculatus* in South America diverged from *G. maculatus* in Tasmania–New-Zealand following the fragmentation of Gondwana and implicate a role for marine dispersal via the West Wind Drift from Tasmania–New Zealand into South America including its surrounding islands [40]. Following the colonization of South America, *G. maculatus* diverged into diadromous populations and multiple resident ones (See [5]).

In a first attempt to describe the phylogeographic patterns in *G. maculatus* from the Southern hemisphere (using allozymes; [58]), authors found minor differentiation between populations from New Zealand and South America. On a more local scale, a study based on allozymes examined the genetic diversity of Patagonian *G. maculatus* [53], finding lower genetic diversity in *G. maculatus* populations inhabiting areas known to have been covered by Pleistocene glaciers than in populations outside the known range of the Last Glacial Maximum (LGM). In a geographically wider attempt to disentangle the main consequences of the Pleistocene glaciations on *G. maculatus*, another study provided evidence of four distinct mtDNA haplogroups (a group of DNA sequences sharing a common ancestor) with some haplotypes shared between populations east and west of the Andes. [35]; Figure 2B,D). Such pattern of genetic diversity is most likely explained by the presence of glacial refugia on both sides of the Andes (reviewed in [59]), the existence of resident and diadromous populations, and importantly, reversals in river drainage from the Atlantic to the Pacific Ocean following deglaciation [35]). Refugial *G. maculatus* populations, exhibiting relatively high genetic diversity, were located mostly in coastal areas along the Pacific coast north of latitude ~42° S where the glaciers did not reach the sea, and on continental areas that remained free of ice during the LGM. *Galaxias maculatus* refugial populations in areas east of the Andes experienced drainage reversals during deglaciation, colonizing systems west of the Andes at latitudes south of 42° S [35]). Demographic reconstructions of *G. maculatus* revealed that populations suffered bottlenecks, decreasing genetic diversity (ca. 1.1–0.6 Myr; Figure 2F), at a time coinciding with the increase in the ice coverage in Patagonia. The genetic diversity of these populations subsequently increased by over 600% from the middle Pleistocene (0.5 Myr) up to the end of the Pleistocene as a consequence of the melting of glaciers and the ensuing increase in the area available for population expansion and colonization [36]).

Other studies on South American *G. maculatus* populations focused on landscape genetics questions. For instance, one study found no genetic differentiation among *G. maculatus* collections within large lakes using microsatellite DNA markers, suggesting that larval and juvenile stages of this species tend to mix in the limnetic zones of lakes [49]. Another study described genetic differences between diadromous and resident *Galaxias maculatus* populations using Single Nucleotide Polymorphic (SNP) markers, with diadromous populations exhibiting higher genetic diversity than resident populations [5]. Diadromous individuals comprise a single genetic group across their Chilean distribution, with some level of fine scale sub-structuring, highlighting their great dispersal ability and presumed lack of site fidelity. An on-going influx of migrants from New Zealand arriving via the West Wind Drift [41,42] cannot be ruled out.

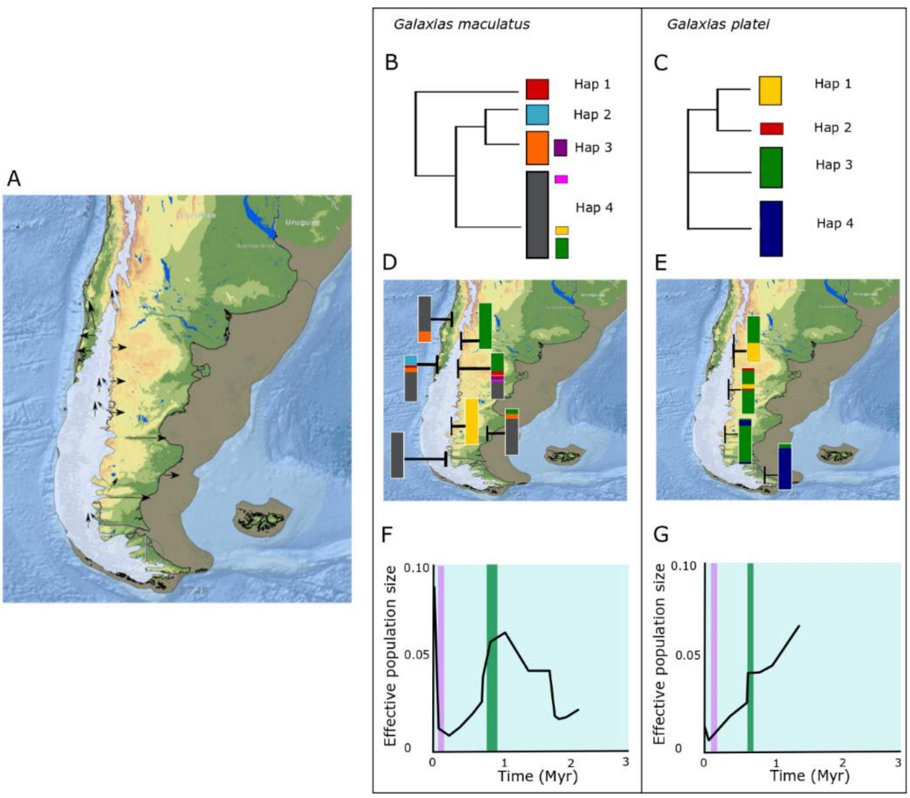

Figure 2. (**A**) Maximum glacial extension during the LGM and glacial refugia for *G. maculatus* and *G. platei*. (**B**,**C**) Schematic representation of mitochondrial haplotype group frequency distribution (estimated with Arlequin) for (**B**) *Galaxias maculatus* and (**C**) *G. platei* (adapted with permission from [34], copyright 2008 Wiley (License 4833120456630) and from [36], Copyright 2011 Wiley (License 4833121089904)). (**B**,**D**) *Galaxias maculatus* haplogroup and sub-group distribution: red (Hap 1 from Central Patagonia west of the Andes, *n* = 16), light blue (Hap 2 from Central Coastal Patagonia, *n* = 9), orange and purple (Hap 3 from Coastal and Central Patagonia, *n* = 32), grey (Hap 4 from west of the Andes, *n* = 211), green (Hap 4 from east of the Andes), pink (Trans Andean) and yellow (Southern Patagonia). (**C**,**E**) *Galaxias platei* haplogroups: yellow (Hap 1 from northern and central Patagonia, *n* = 12), red (Hap 2 from Central Coastal Pacific Patagonia, *n* = 3), green (Hap 3 from northern to southern Patagonia, *n* = 15), and blue (Hap 4 from southern Patagonia, *n* = 20). Haplogroup frequencies are shown in bars in panels (**D**) (*G. maculatus*) and (**E**) (*G. platei*). (**F**,**G**) skyline plots reflecting changes in genetic diversity (based on effective population sizes) for (**F**) *G. maculatus* and (**G**) *G. platei*. The timing of the Last Glacial Maximum and of the Coldest Pleistocene Glaciation are indicated by the pink and green bars in panels (**F**,**G**), respectively (Adapted from on [36]).

Genetic diversity and differentiation patterns are generally the results of both historical and contemporary processes. For instance, microsatellite markers revealed that *G. maculatus* populations from northern Patagonia exhibit higher genetic diversity and are more highly differentiated (within watersheds) that *G. maculatus* populations from Southern Patagonia, a pattern explained by the lesser effects of glaciations in northern than in southern Patagonia [6]. West of the Andes in Chile, DNA sequence diversity patterns indicate that estuarine *G. maculatus* exhibit relatively low genetic differentiation over 1500 Km of coastal waters south of 42° S, where the glaciers reached the sea during the LGM, a pattern that contrasts with *G. maculatus* populations north of 42° S [35,44–46].

On a more local scale, a study using mtDNA analyzing estuarine and Andean populations from a single river system found that individuals from the estuarine population were more genetically diverse and more salinity tolerant than individuals collected from the Andean population [46]. The observed genetic pattern was attributed to a decline in diversity in the Andean population during the glaciations, compared to the estuarine population that survived in unglaciated areas [46]. A similar pattern was observed in a recent study by comparing mtDNA sequences from individuals from one resident and one diadromous *G. maculatus* population in the southern limit of the species distribution in Tierra del Fuego, Argentina [7]. Despite the short distance separating the resident from the diadromous estuarine population, the resident population exhibited lower genetic diversity than the diadromous one [7]. The observed higher genetic diversity in estuarine *G. maculatus* populations found by both studies [7,46] could also be explained by incoming gene flow from neighboring populations, increasing the genetic diversity of estuarine populations. The lower diversity observed in Andean and isolated lakes is consistent with isolation combined with the effects of glaciations, both reducing the effective population sizes of these populations.

3.2. *Galaxias platei*

The uplift of the Andes and the glacial cycles of the Quaternary influenced genetic diversity and divergence patterns in *G. platei* as much as they did for *G. maculatus.* A study using DNA sequences discovered the presence of four main haplogroups, with two haplogroups exclusive to *G. platei* populations west of the Andes and two groups shared between populations east and west of the Andes in Central and Southern Patagonia [34], but absent in the Chilean northern Patagonian distribution (Figure 2C,E). DNA sequence diversity suggests that the split between eastern and western *G. platei* populations most likely took place ca. 1.5 Myr. Unlike the changes in long term effective size observed in *G. maculatus*, the effective size of *G. platei* populations were constantly reduced during the Quaternary. By the end of the Pleistocene, and likely as a consequence of the reduction in available habitat during glacial times, the long term effective size of *G. platei* was merely a 16% of the extant population size [36,50]; Figure 2G). During the Holocene, with the melting of the glaciers, *G. platei* experienced a rapid expansion, colonizing previously glaciated areas. In general, DNA sequences and microsatellite markers show that *G. platei* populations appear to have survived in non-glaciated areas east of the Andes, in small local refugia west of the Andes within the region thought to have been covered by glaciers, and west of the Andes north of latitude 42° S where the glaciers did not reach the sea during the LGM [22,34,36,39]. The temporal pattern of colonization likely varied with latitude and the particular characteristics of the focal system. For instance, a study using microsatellites to estimate divergence time and changes in migration patterns revealed that mountain lakes in northwestern Patagonia west of the Andes (San Pedro River, Valdivia River watershed) appear to have been colonized only during the late Holocene (720–2040 years BP); Figure 3A; [39];) following drainage reversals that took place when glaciers, which previously had acted as barriers to western dispersal, began melting (similar episodes of drainage reversals were documented for other species as well using DNA sequences and microsatellite markers, see [52,60]). Further south, in central Andean Patagonia, studies using microsatellite markers and DNA sequences suggest that *G. platei* populations likely also survived the Pleistocene glaciations in areas east of the Andes, and colonized western Andean systems during the Holocene [22,34]; Figure 3B). This pattern of colonization, however, seems not to be a rule, since in southernmost Patagonia, *G. platei* appears to have survived in situ in a large paleolake with population differentiation taking place simultaneously with the lowering of the paleolake level and its fragmentation into a number of extant lakes as glaciers melted (1400–7800 years BP; Figure 3C; [38]). By comparing divergence times obtained through molecular methods (based on microsatellite markers) with the geomorphological evidence for the appearance of extant lakes in the Serrano system in southernmost Patagonia, population fragmentations seemed to fit well with the chronological appearance of the lakes [38]).

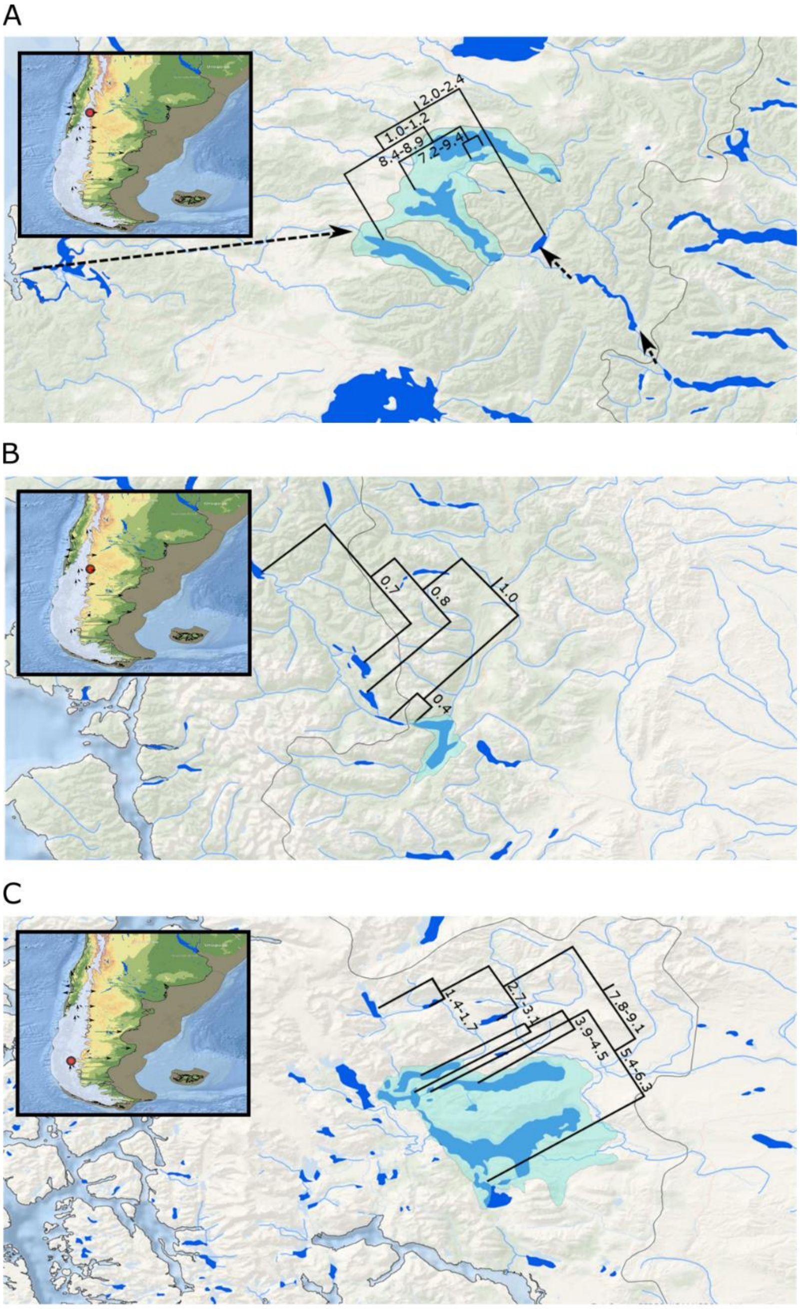

Figure 3. Population divergence times (in thousand years before present) of three *G. platei* populations from southern Patagonia (Adapted with permission from [22], copyright 2018 Wiley (License 4879110347629) and from [38], copyright 2015 Wiley (License 4833140056366)) including the San Pedro River (**A**), Puelo River (**B**) and Serrano River basin (**C**). The location of the rivers in Chile can be found in Figure 1. Dashed lines show likely colonization routes in **A**. Light blue areas show the extension of paleolakes. Red circles in each reference map in the upper left corner show the location of the river basin.

3.3. *Aplochiton*

The existence of three *Aplochiton* species has been historically questioned, with two species, *A. taeniatus* and *A. zebra*, widely validated, and *A. marinus* usually assumed as a synonym of *A. taeniatus* [61,62] due to the lack of distinguishable characteristics. The first genetic study on *Aplochiton* species showed no evidence of the existence of *A. marinus* [43], yet this conclusion was apparently reached without collections from the area where *A. marinus* has presumably been recorded in the past [Calle Calle river (Lat 39.80° S) in the Valdivia River watershed]. A second study, combining morphological and genetic analyses on *Aplochiton* species within northern and southern Patagonia in Chile [32], provided evidence consistent with the existence of *A. marinus.* This study revealed that *A. marinus* was unambiguously identified at a morphological and genetic level, but it also revealed that *A. zebra* and *A. taeniatus* were only weakly distinguishable using morphology; genetic tools were needed to identify both species. The same authors showed that at a phylogeographic scale, *Aplochiton* species displayed a lack of structure and uncorrelated geographic genetic distance among populations. A subsequent study based on *A. zebra* mtDNA (16S and COI) sequences and nuclear microsatellite markers described evidence of population structure as highly correlated with drainage system [52]. The disparity between approaches likely reflects the fact that studies based on mtDNA sequences reveal long-term historical processes and little differentiation within *A. zebra* and *A. taeniatus*, while analyses based on microsatellite markers reveal short-term historical patterns, including species or lineage differentiation, suggesting *A. marinus* is a real entity with a relatively recent origin.

4. Discussion

4.1. Phylogenetic Position of South American Galaxiids

The most recent phylogenetic reconstruction of galaxiids from throughout the world [42] formulated the most extensive phylogeny of the family to date. That phylogenetic reconstruction, however, opens up new questions on the divergence of South American species, since the origin of these species is likely explained by several events, including multiple colonization events from Australia–New Zealand followed by the loss of marine dispersal ability for some species. The loss of marine dispersal followed by geographic and reproductive isolation can lead to speciation, as has been described for some galaxiid species in New Zealand [63]. For instance, *G. maculatus* resident populations showed clear phenotypic differences in size [64], vertebral count and fecundity [65] from the migratory or diadromous populations. These differences led earlier researchers [66] to suggest that *G. maculatus* resident population from one lake, Lake Riñihue, could be considered a separate species, *G. alpinus.* Although subsequent mtDNA studies do not support the presence of a new species, recent genomic work provides evidence that resident populations in the northern part of the species range are highly differentiated from their diadromous counterparts [5]. Further studies on the genomic mechanisms of diadromy and its loss, and the levels of genomic differentiation in other galaxiids resident *G. maculatus* populations, including populations from the various ancestral haplogroups [35,36], can help assess the extent of galaxiid genetic diversity in Patagonia.

4.2. Genetic Diversity: The Role of Contemporary Impacts of Human Activity

Although orogeny and glaciations played a major role in extant patterns of genetic diversity in galaxiid and other native Patagonian fishes [50,60,67,68], more recent processes, such as the introduction of invasive species (e.g., salmonid species) and the construction of dams for hydroelectric power generation, have likely had a greater influence on the genetic patterns of galaxiid fishes from South America than has been recognized thus far. Some authors have found a slight negative correlation between salmonid abundance and microsatellite diversity (heterozygosity and allelic richness) in *Aplochiton zebra*, but have not find a correlation between salmonid abundance and mtDNA diversity [52]. This result is to be expected as changes in genetic diversity can hardly be expected when populations remain large (thousands of individuals) and the method used is mtDNA, as the effects of these events can more effectively be traced with microsatellites and SNPs. *Galaxias platei*, a species with smaller effective population sizes than *G. maculatus*, were indeed found to be affected by invasive salmonids [39]: three genetic diversity indices (number of alleles, allelic richness and observed heterozygosity) were lower in populations coexisting sympatrically with salmonids than in *G. platei* populations inhabiting lakes without salmonids [39]. Thus, the contemporary genetic diversity in *G. platei* populations can largely be explained by the combined effects of divergence time (during the Holocene) and the presence/absence of salmonids [39]. The decline in genetic diversity in some galaxiid fishes is likely the result of ecological mechanisms, such as trophic interference [24,69,70]. For instance, the diets of *G. platei*, *A. zebra*, and *A. taeniatus* appear to differ between salmonid-invaded and non-invaded lakes [24,33]. Under the presence of salmonids, the ecological niche of galaxiids is generally strongly reduced due to competition and predation, leading to the reduction and, in some cases, even the collapse of local populations [71].

The presence of salmonids in Patagonian lakes is not the only factor affecting the ecological and genetic patterns of galaxiids. Dams have also produced great changes in watersheds, and their ecological effects on fishes is well documented (e.g., [72–75]). As expected, dams can also affect fish genetic diversity patterns, but these are generally manifested only after a time lag that is a function of the life history characteristics of the species of concern, including its generation time and its population effective size [22]. For instance, authors have found that the construction of a dam in the early 1960s has not affected the genetic diversity of *G. platei* populations in a river system in Northern Patagonia [38]. Subsequently, however, the same authors, using forward-in-time simulations, showed that changes in the genetic diversity of *G. platei* can only be detected 50–80 years after the construction of the dam, when a sudden reduction in population size and a loss of genetic diversity takes place [22]. Similar results are likely to be found with other galaxiid species, and the fact that a high number of dams are planned for construction over the next decades in South America suggests it is imperative to explore the potential consequences of these habitat alterations for the other species in the group. For example, *Galaxias maculatus* is sympatric with *G. platei* throughout much of their distributions in South America [2,30]. Given the life history of *G. maculatus* and its high genetic diversity, it has been hypothesized that the construction of dams would have fewer impacts on *G. maculatus* than on *G. platei* (e.g., [47]. However, the idiosyncratic patterns of genetic diversity within each basin should be considered to understand how a dam will affect each species. As shown by a recent study [5], northern resident populations of *G. maculatus* are highly differentiated from both their diadromous counterparts inhabiting the estuarine areas of the same river basins as well as from neighboring resident populations. Therefore, impacts on these populations should be analyzed separately in environmental impact assessments of hydropower projects. In addition, *G. maculatus* resident populations inhabiting upstream river zones, often most affected by the habitat alteration that follows dam construction and the development of man-made reservoirs, are generally also affected most by introduced salmonids. The cumulative and synergistic impacts of these different stressors in South American galaxiids needs to be addressed quickly in order to conserve these species in lakes and rivers [76].

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