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Exotic species modify the functional diversity patterns of freshwater fish assemblages in continental Chile: Examining historical and geographical patterns



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ABSTRACT

The Neotropical region is an important reservoir of functional diversity of freshwater fish in the world. Recent studies have shown that functional and taxonomic diversity in this region has increased as a consequence of the introduction of exotic species. However, little is known about how this phenomenon has modified functional diversity at the watershed level. In the present study, we analyze the spatio-temporal changes of functional diversity in 22 watersheds of continental Chile, hypothesizing that the introduction of exotic species could have contributed to increasing and homogenizing the functional diversity within and among watersheds. Toward this purpose, we implemented measures of functional diversity (F_{Ric}), β -diversity (F_{Div}), turnover (F_{Tur}), and nestedness (F_{Nes}) in two compositional stages, which we call "historical" and "current". The former considered the most probable composition of native species prior to European colonization, while the latter considered the current distribution of native and exotic species. For these two stages, we determined the changes in (F_{Ric} , F_{Div} , F_{Tur} , and F_{Nes}) between pairs of watersheds, as well as the effect of geographic distance. Our results showed that, on average, F_{Ric} has increased its historical value by 156%; on the other hand, ΔF_{Div} and ΔF_{Tur} decreased significantly from its historical composition to current one ($\Delta F_{Div} = -7.4\%$; $\Delta F_{Tur} = -13.2\%$; both $P < 0.05$), while nestedness showed no significant changes ($\Delta F_{Nes} = -3.6\%$; $P > 0.05$). Finally, geographic distance between watersheds was negatively and significantly correlated with change in β -diversity and spatial turnover ($r = -0.267$; $r = -0.410$, respectively; both $P < 0.05$), while ΔF_{Nes} did not show a significant correlation with distance ($r = 0.178$; $P > 0.05$). These results indicate that exotic species (a) have increased functional diversity in local assemblages, because they display historically absent functional features; and (b) have promoted functional homogenization between assemblages, which is more intense between geographically more distant ones. These findings suggest that, due to their functional features, the presence of exotic species poses a probable risk for the functional stability of watersheds in continental Chile, and that it is necessary to implement conservation measures to protect this unique fish fauna.

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1. Introduction

Most of the world's freshwater fish assemblages are undergoing a biotic homogenization process (Toussaint et al. 2016, 2018). This phenomenon is determined mainly by the introduction of new species (i.e., exotic) and the extinction of native taxa (McKinney and Lockwood 1999; Olden and Rooney 2006). At present, biotic homogenization is conceived as a multifaceted phenomenon (Olden et al., 2018) in which changes in the taxonomic composition of the assemblages carry over modifications of the functional and evolutionary diversity (Villéger et al., 2017). Because the causes of biotic homogenization are closely related to anthropic activities, there has been a growing interest in analyzing their ecological consequences beyond the taxonomic dimension (Villéger et al., 2017; Olden et al., 2018).

The functional diversity of an assemblage can be defined as the representation of functional features of the species that make it up (Villéger et al., 2013). Because these traits not only contribute to the persistence of species in the community, but also integrate them into ecological processes, the functional diversity of the assemblage will be modified as a result of extinction/invasion events (Pool and Olden 2012; Villéger et al., 2014). Therefore, the arrival or extinction of species that carry functionally novel or redundant features to the assemblage ends up impacting the ecological processes of which these species are part (Díaz and Cabido 2001). This factor puts the ecological integrity of communities at risk (Díaz and Cabido 2001; Olden et al., 2004), affecting the provision of environmental services supplied by freshwater ecosystems to humans (Clavel et al., 2010; Petsch 2016). By extension, if the functional diversity of two or more initially different assemblages tends to converge, then it becomes possible to show the occurrence of homogenization in their functional dimension (Villéger et al., 2014).

Currently, spatial or β -diversity, is conceived as a key indicator for unveiling homogenization and the underlying processes (Baselga and Orme 2012; Carvalho et al., 2012; Villéger et al., 2013). Indeed, its components, labeled turnover and nestedness (Baselga and Orme 2012), reveal the occurrence of two antithetical processes (Baselga 2010; Almeida-Neto et al., 2008; Carvalho et al., 2012). On the one hand, species turnover corresponds to changes in diversity in response to environmental gradients (current or historical), which filter the composition of those assemblages (Baselga 2010; Chase et al., 2011), while nestedness is associated with changes in diversity due to loss or gain of species (Lennon et al., 2001; Vellend 2001; Legendre 2014). For this reason, the study of β -diversity and its turnover and nestedness components can help to understand the role of these processes in configuring the functional diversity of assemblages, at the same time revealing the mechanisms that underlie homogenization.

The Neotropics concentrate a large proportion of the functional richness described among freshwater fish in the world (Toussaint et al., 2016). Nevertheless, this diversity -as well as the taxonomic one-is not homogeneously distributed in the region (Toussaint et al., 2018). Continental Chile, for example, which has an extensive and unique latitudinal arrangement, harbors a comparatively small species richness ($n = 46$) distributed heterogeneously along the territory (Vila and Quizada-Romagioli 2018). In terms of functional diversity, these fish species are characterized by having a small body size (<20 cm long), a diet specialized in invertebrates, and a morphology adapted to fast running rivers with a high grade (Vila and Habit 2015). This scenario contrasts with the functional diversity observed among the exotic species introduced to Chile (Rojas et al., 2019), on account of their reaching larger body sizes (>30 cm), having generalized diets, and traits that favor greater vagility and colonizing ability (Habit et al., 2015). Although recent studies have shown that exotic species have contributed to homogenizing the taxonomic composition of the watersheds of continental Chile (Castro et al. 2014, 2020; Rojas et al., 2019), to date there are no reports regarding the trends that functional diversity has followed.

Here, we analyze whether recent invasion and extinction events of freshwater fish species have promoted changes in the functional diversity among watersheds of continental Chile. Specifically, we will try to determine if these assemblages are in the process of functional homogenization, discriminating between their replacement components and spatial nestedness. Thus, we will try to understand how the functional attributes that characterize the assemblages of each watershed have been modified as a result of the presence of exotic species, and whether this factor yields a functional homogenization process along the extensive latitudinal gradient studied.

2. Materials and methods

2.1. Watersheds studied

We studied 22 of the 101 watersheds recognized in continental Chile (DGA 2020). Together, these watersheds represent 21% of the country's total and cover about 32% of the area of the continental territory. The watersheds were Huasco, Elqui, Limarí, Choapa, Aconcagua, Maipo, Rapel, Mataquito, Maule, Itata, Andalién, Biobío, Imperial, Toltén, Valdivia, Bueno, Baker, Maullín, Palena, Cisnes, Aysén, and Serrano (Fig. 1). All these watersheds are part of a geomorphological continuity of over 2462 km long along the western slope of the Andes mountain range; all of them are exorheic, carrying their waters from the Andes to the Pacific Ocean on the west.

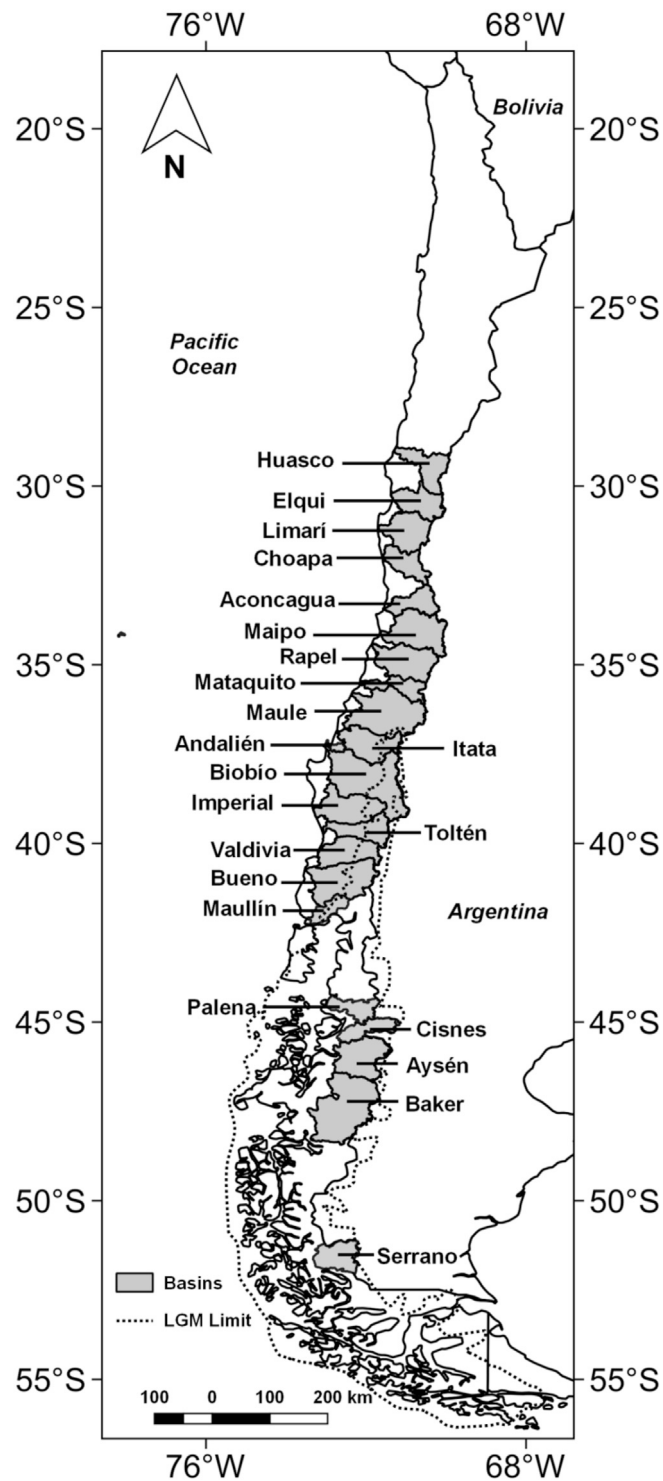


Fig. 1. Geographic location of the 22 studied basins of Chile. In gray shade the analyzed basins. The dotted line represents limits of the Last Glacial Maximum (LGM) in the basins of Chile, from Villagrán, 2001.

2.2. Fish species distribution

For each watershed, we recorded the composition of native and exotic fish species, conducting an exhaustive literature review of scientific publications and technical reports, both public and private. This review included publications between the years 1927 and 2017, totaling 93 documents (more details in Rojas et al., 2019). Based on the information obtained, we managed to configure the most probable composition of fish assemblages before (historical) and after (current) the Spanish colonization that began in 1541. This allowed us to develop two species \times watershed matrices, which were called matrices H and C, respectively. The historical matrix included the most probable composition of native fish (for 31 out of 46 species) before the Spanish colonization, while the current matrix represented the present composition, encompassing native -now 30 species due to the extinction of *Diplomystes chilensis* (Arratia and Quezada-Romegialli 2017)- and exotic species (now 28). In these matrices, the distribution of species per watershed was scored with 1 to denote their presence and 0 to denote their absence.

2.3. Functional traits

Following Matsuzaki et al. (2013), we recorded the status of nine functional traits for the 59 species present in our matrices. These features were used according to the information availability for all studied species: a) body size, b) barbel type, c) mandibular protractibility, d) presence of scales, e) type of migration, f) body shape, g) adult diet, h) adult in vertical position in the water column, i) number of eggs (see Annex 1). All these features correspond to attributes of life history and trophic ecology of freshwater fish, directly associated with the performance of ecological roles within each assemblage (Villéger et al., 2010). The information regarding the character status for each species was obtained from FishBase (www.fishbase.org; Froese and Pauly, 2019), in addition to the information available in Vila et al. (1996, 1999, 2006), Habit et al. (2006, 2015) and Link and Habit (2015), in the case of native species. Except for body size (a continuous variation feature), all traits had an ordinal variation (see Annex 1). The distribution of traits and their characters for each species is shown in Annex 2. It is important to note that the specific use of these nine traits was conditioned by the need to have comparable information for both native and exotic taxa; reason why other features (e.g., year of sexual maturation, maximum age of survival, and reproductive strategy) used by similar studies (e.g., Villéger et al., 2013; 2017; Su et al., 2015), could not be included here due to the lack of information on native species.

2.4. Functional richness and β -diversity

The functional richness (F_{Ric}) of any assemblage (A_i) can be conceived as the convex volume generated by the graphic representation of the set of morpho-functional characters of each of the assemblage's species (Cornwell et al., 2006). Using the Gower (1971) distance we prepared a morpho-functional dissimilarity matrix between each pair of species, calculating the Euclidean distances among the morpho-functional attributes indicated in the previous section. A Principal Coordinates Analysis (PCoA) was applied to this matrix, allowing the calculation of the volume of the convex cover of each assemblage based on the first three main axes (Villéger et al., 2008). Thus, for example, $V(A_1)$ and $V(A_2)$ correspond to the convex cover volume of assemblages A_1 and A_2 , respectively, while $V(A_1 \cap A_2)$ corresponds to the volume of the shared or intersected convex hull (Villéger et al., 2013).

To calculate functional β -diversity (F_{Div}), we used the following algorithm: $F_{Div} = [(V(A_1) + V(A_2)) - 2 V(A_1 \cap A_2)] \cdot [(V(A_1) + V(A_2) - V(A_1 \cap A_2))]^{-1}$ (Villéger et al., 2013), where $V(A_1)$ and $V(A_2)$ represent the multidimensional volumes of assemblages A_1 and A_2 , and $V(A_1 \cap A_2)$ represents the multidimensional volume shared by both assemblages (Villéger et al., 2013). Then, we disaggregated F_{Div} into turnover and nestedness components. The functional turnover was calculated as: $F_{tur} = [2 \min(V(A_1), V(A_2)) - 2 V(A_1 \cap A_2)] \cdot [(2 \min(V(A_1), V(A_2)) - V(A_1 \cap A_2))]^{-1}$ (Villéger et al., 2013); nestedness was calculated as $F_{nes} = [(|V(A_1) - V(A_2)|) \cdot V(A_1 \cap A_2)] \cdot ((V(A_1) + V(A_2) - V(A_1 \cap A_2))) \cdot [(2 \min(V(A_1), V(A_2)) - V(A_1 \cap A_2))]^{-1}$ (Villéger et al., 2013). F_{Div} , F_{tur} and F_{nes} were applied on historical (H) and current (C) matrices thus obtaining $F_{Div,H}$; $F_{Div,C}$; $F_{tur,H}$; $F_{tur,C}$; $F_{nes,H}$; and $F_{nes,C}$. These indices oscillated between 0 and 1, denoting minimum and maximum values, respectively. All the calculations were made using the "geometry" and "rcdd" library of R (Villéger et al., 2013).

2.5. Analysis

To determine functional homogenization between watersheds, we analyzed the distribution of differentials for β -diversity ($\Delta F_{Div} = F_{Div,C} - F_{Div,H}$), turnover ($\Delta F_{tur} = F_{tur,C} - F_{tur,H}$), and nestedness ($\Delta F_{nes} = F_{nes,C} - F_{nes,H}$), calculated between pairs of watersheds at two different times (current and historical). It was established that a distribution of differentials whose median was statistically less than zero (<0), was consistent with a functional homogenization process, because it indicates a significant decrease of the current spatial change with respect to the historical one. Alternately, a positive median (>0) denotes the occurrence of functional differentiation, consistent with assemblages that are functionally more different at present than in the (historical) past. A median not different from zero (≈ 0) denotes lack of significant changes in functional diversity patterns (Villéger et al., 2013). To evaluate the statistical bias of the median we used the signed-paired ranges Wilcoxon test.

With the purpose of evaluating the effect of geographic distance on the values of β -diversity, turnover, and nestedness, these values were correlated with the distance between the pairs of watersheds. This distance (km) was determined as the

separation between the geometric centers of each watershed, using QGIS version 2.18. The distance between pairs of watersheds was registered in a distance matrix (D) and its effect was analyzed by applying the Mantel test (Smouse et al., 1986).

3. Results

The analysis of species composition in historical times showed that the taxonomic richness of native fish varied between 10 and 16 species per basin, between latitudes 35 and 40°S (Fig. 2A, closed circles). Between latitudes 28 and 35°S, and between 40 and 55°S, richness was lower, between 4 and 6 species per basin (Fig. 2A, closed circles). A similar variation pattern was observed when analyzing the latitudinal distribution of functional diversity ($F_{Ric,H}$), which ranged from 0.008 to 0.01 between latitudes 35 and 40°S (Fig. 2B, closed circles), declining to values lower than 0.0001 towards north and south ends of the studied range (Fig. 2B, closed circles). Taxonomic and functional richness were significantly correlated ($r = 0.931$; $P < 0.05$), showing that the greater the richness, the greater the functional diversity.

The current assemblages showed an increase in taxonomic richness, between 20 and 28 species per basin between latitudes 35 and 40°S (Fig. 2A, open circles), and between 9 and 16 species per watershed between 28 and 35°S and between 40 and 55°S (Fig. 2A, open circles). This increase is due to the presence of exotic species, which have increased by 1.6–2.6 times the historical richness per basin (current richness/historical richness). Functional diversity $F_{Ric,C}$ varied between 0.001 and 0.04, showing an increase in its magnitude in all the watersheds (Fig. 2B, open circles). Although the correlation between taxonomic and functional richness decreased with respect to the historical condition, it was still positive and significant ($r = 0.857$; $P < 0.05$).

β -functional diversity calculated in historical ($F_{Div,H}$) and current ($F_{Div,C}$) times ranged between 0.0 and 1.0 in both cases (Fig. 3A); the distribution of the differential values ΔF_{Div} showed a median significantly less than zero ($T = 6.8$; $P < 0.05$; Fig. 3A). Similarly, the distribution of the turnover differentials (ΔF_{Tur}) also showed a median significantly less than zero ($T = 11.3$; $P < 0.05$), while the nestedness differentials (ΔF_{Nes}) did not show a median different from zero ($T = 2.1$; $P > 0.05$; Fig. 3). These results show a significant reduction in β -diversity from historical periods to date, associated with the component of distributional turnover but not with nestedness, which denotes functional homogenization between the studied basins.

Finally, the geographic trend analysis of the changes in β -diversity (ΔF_{Div}) and its components (ΔF_{Tur} and ΔF_{Nes}) showed two types of behavior for these indices (Fig. 4). On the one hand, both ΔF_{Div} and ΔF_{Tur} exhibited significant and negative correlations with spatial distance ($r = -0.267$; $r = -0.410$, respectively; Mantel test in both cases $P < 0.05$). On the other hand, changes in nestedness were positively correlated with geographic distance, although this trend was not significant ($r = 0.178$; $P > 0.05$; Mantel test). These results indicate that the decrease in β -functional diversity and spatial turnover was greater (in absolute terms) when comparing increasingly distant basins.

4. Discussion

Up to now, total richness of freshwater fish species in Chile (i.e., gamma-diversity) has increased from 31 to 59 taxa in the 22 studied basins, i.e., a 90% increase in regional taxonomic diversity. At the individual watershed level, the observed increase has been slightly higher, as the average richness grew from 9 to 18 species, an increase equivalent to 100% of the original diversity. This scenario is a consequence of the introduction of 28 exotic species (Camus and Jaksic 2009; Habit et al., 2015), whose ecological and functional effects are poorly understood to date, so that our study constitutes a first advance to elucidate them.

Although the average taxonomic richness of the watersheds has doubled (from 9 to 18 species), the increase in functional diversity (F_{Ric}) has been on average around 150%. At least two implications follow. First, functional diversity in watersheds depends on taxonomic changes, but is not necessarily associated in a 1:1 ratio; in fact, several studies have shown that after introduction of new species, functional diversity increases disproportionately with respect to the increase in richness (Villéger et al., 2014; Toussaint et al. 2016, 2018). Second, this increase in functional diversity shows that the set of exotic species present has novel functional features, not represented in the native assemblages (Pool et al., 2016; Toussaint et al., 2018). Indeed, native and exotic species differ in varied functional traits, the most conspicuous and characteristic studied here being body size and food habits (see below).

Although it is generally accepted that an increase in functional diversity contributes to greater ecological stability for watersheds (Yashi and Loreau 1999; Tilman 2001), this may not be the case in our study system. Indeed, 21 of the 28 exotic species have general food habits and can prey on native species (Habit et al., 2015; Vila and Quezada-Romegialli 2018). This poses a risk to the ecological stability of the assemblies, because close to 90% of the native species have a compromised conservation status (MMA, 2018). Thus, a likely future compositional scenario is the extirpation or extinction of native fish populations due to predation (or competition for habitat) by exotic species, which could contribute to the decrease in taxonomic and functional diversity (Rojas et al., 2019), and probably to increase taxonomic and functional homogenization (see below). Some studies have already reported events of extirpation of native taxa in certain tributaries of some watersheds in southern Chile, and although the specific causes have not been determined, all these cases are associated with the presence of exotic species (Habit et al. 2010, 2015).

Changes in β -diversity (ΔF_{Div}) between watershed pairs showed an average decrease of 7.5%, a statistically significant reduction in functional turnover ($\Delta F_{Turn} < 0$), but not in nestedness ($\Delta F_{Nes} \approx 0$). These findings indicate a process of functional

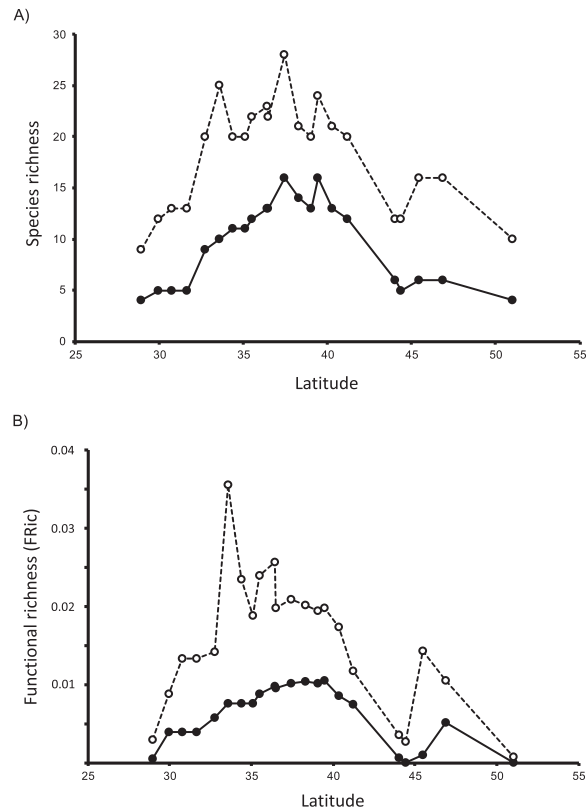


Fig. 2. Historical (closed circles) and current (open circles) taxonomic richness along the latitudinal gradient in panel A; and historical (closed circles) and current (open circles) functional richness (F_{Ric}) in panel B. Despite their closeness to the x-axis in the cases of the Cisnes and Serrano basins, these two datapoints differ from zero ($0 < F_{Ric} < 0.0001$).

homogenization in which the historically established functional diversity between the watersheds has been converging until today (Olden et al., 2018). Interestingly, this decrease in β -functional diversity was greater than that observed in taxonomic terms ($\Delta\beta$ -diversity = -2.1% ; Castro et al., 2020), a phenomenon also documented in other watersheds of the globe (Villéger et al., 2014; Su et al., 2015).

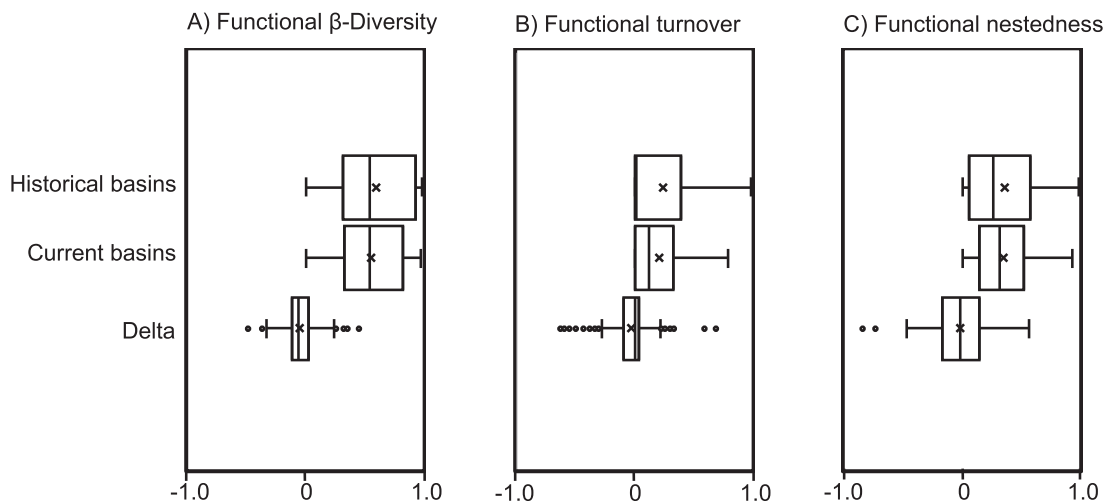


Fig. 3. Box plots for distributions of functional β -diversity, functional turnover, and functional nestedness, showing their temporal differentials (ΔF_{Div} ; ΔF_{Tur} ; ΔF_{nes}). The boxes represent the maximum and the minimum values indexes; the interior line of the box indicates the median and "x" is the arithmetic mean.

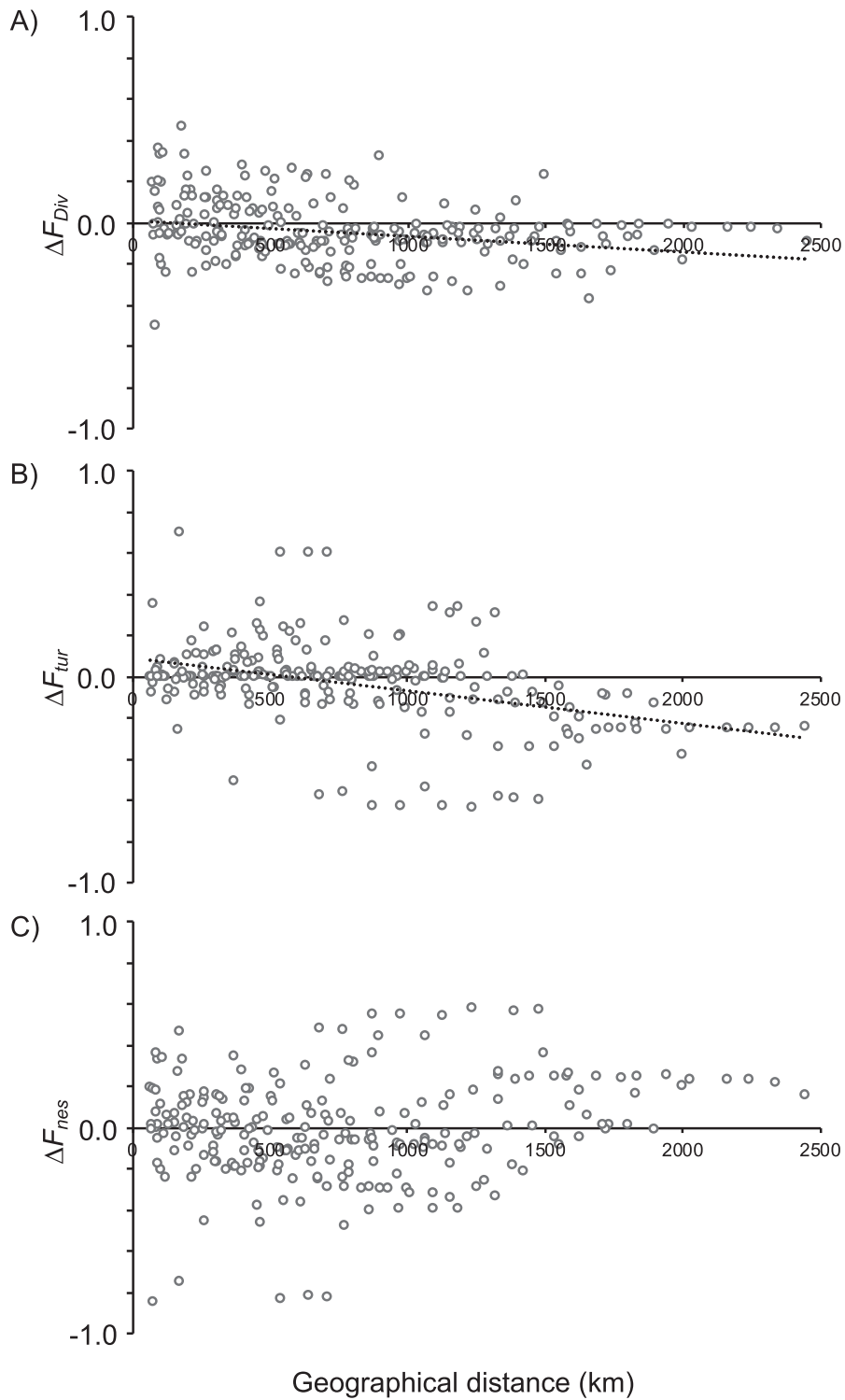


Fig. 4. Geographical correlation for changes in functional β -diversity (ΔF_{Div} ; panel A), functional turnover (ΔF_{tur} ; panel B), and functional nestedness (ΔF_{nes} ; panel C).

The hypothetical extinction of native species with a compromised conservation status may contribute to increase functional homogenization, given that they display unique features in the assemblages (Toussaint et al., 2014). This can be

evaluated, for example, considering species of the genera *Diplomystes* and *Nematogenys*, which occupy a small number of basins (Rojas et al., 2019) and which have relatively specialized and unique functional traits (demersal habits, as well as a diet specialized in zoobenthos; see Annex 2). Therefore, their removal/extinction could lead to the loss of functional diversity in the basins, which will convey functional homogenization between them. These conditions, in which native species show unique and distinctive roles and functional traits, whose potential extinction could exacerbate the homogenization of these basins, constitutes a scenario that has been proposed for basins in other regions of the world (Mouillot et al., 2013; Leitão et al., 2016; Toussaint et al., 2018). With this, it is expected that homogenization in its taxonomic, functional and evolutionary dimensions, will increase in the future. Therefore, it is possible to speculate that the functional homogenization detected for the Chilean basins is part of a larger-scale regional trend observed in other South American basins (Toussaint et al., 2018).

From the standpoint of the latitudinal gradient examined, taxonomic diversity of the historical assemblages followed a pattern of peak richness between 26 and 30°S, and then a decrease from 40°S southwards (see Fig. 1). This phenomenon has been associated with the occurrence of geological events (emergence of the Andes mountain range 20 million years ago; Seyfried et al., 1998) and climatic events (Last Glacial Maximum, 20 thousand years ago; Hulton et al., 2002; Habit and Victoriano 2012), which have reduced the taxonomic richness in both ends of the country (between latitudes 18 - 30°S and 40 - 58°S), maintaining a greater richness at intermediate latitudes (30 - 40°S; Figueroa et al., 2013; Vila and Habit 2015). This latter latitudinal range is particularly important, because most of the exotic species introduced to the country are concentrated here (Vila and Habit 2015). The decrease in native richness from 40°S onwards has been associated with the glacial history of the region (see Fig. 1), which affected this territory extensively (Hulton et al., 2002). Thus, the richness of native species south of latitude 40°S could be the result of post-glacial colonization from “refuge” areas (Cussac et al., 2004; Pascual et al., 2007). In addition to the above, our results suggest that the LGM also affected the functional diversity of fish that currently exist in these watersheds, given that their magnitude ($F_{Div,H}$) also declines from latitude 40°S. These results also suggest that the watersheds of the extreme south of Chile can be considered unsaturated assemblages from a functional point of view, a condition that could facilitate the establishment of exotic taxa and favor the establishment of future inoculations.

As a complement of the above, changes in β -diversity (ΔF_{Div}) and spatial turnover (ΔF_{Tur}) were negatively correlated with geographic distance, implying that the decline in β -diversity and functional turnover increases with geographic distance between watersheds. These findings indicate that the functional homogenization process is more intense between more geographically distant basins, probably as a result of low richness of native species in watersheds located at extremes of continental Chile, and the introduction of a similar set of exotic species (e.g., *Gambusia affinis*, *G. holbrooki*, *Australoheros facetus*, *Oncorhynchus mykiss*, and *Salmo trutta*), which have reached a wide distribution in Chile.

In summary, Chilean freshwater fish assemblages currently harbor a diversity of exotic species that have contributed to increase their functional diversity, beyond what is determined by taxonomy. As a result, these basins are in transit towards functional homogenization, as a consequence of the introduction of a similar set of species throughout the different basins, a process also recorded at the regional (South America) and global scales. The possible extinction of their native taxa (90% of which have a compromised conservation status) constitutes a risk for the functional stability of the watersheds in the near future, forecasting a reduction in functional diversity and an increase in functional homogenization between watersheds.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2020.e01355>.

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