Original Articles

Exotic species elicit decoupled responses in functional diversity components of freshwater fish assemblages in Chile

Pablo Rojas [a], Sergio A. Castro [b,*], Irma Vila [a], Fabian M. Jaksic [c]

[a] *Departamento de Ciencias Ecológicas, Universidad de Chile, Santiago, Chile*
[b] *Laboratorio de Ecología y Biodiversidad, Universidad de Santiago de Chile, Alameda Bernardo O'Higgins 3363, Santiago, Chile*
[c] *Center of Applied Ecology and Sustainability (CAPES), Pontificia Universidad Católica de Chile, Av. Libertador Bernardo O'Higgins 340, Santiago 8331150, Chile*

ABSTRACT

In the freshwater basins of central Chile, 28 exotic species have been introduced, which have contributed to increase taxonomic diversity. Nevertheless, how these species have modified the components of functional diversity in these assemblages, a key aspect in learning about their present and future stability within an ecosystem, is unknown. In this study, we analyzed how the introduction of exotic species affects the functional diversity components of richness (FRic), divergence (FDiv), specialization (FSpe), and functional originality (FOri). Additionally, we simulated the effect of the loss (extinction/extirpation) of threatened native species. To do so, we gathered information on the distribution and functional characters of native and exotic species. Through Principal Coordinates Analysis (PCo), we obtained three independent axes (PCoA1, PCoA2, and PCoA3), which allowed us to define a multidimensional space and then to calculate FRic, FDiv, FSpe, and FOri. Our results indicate that richness and functional originality have increased significantly with the introduction of exotic species (263% and 32%, respectively). In contrast, functional divergence and specialization have remained the same. The possible extinction of threatened native species may promote increases in functional originality, decreases in functional richness and divergence, and unchanged functional specialization. On the other hand, a subset of exotic species presents novel features, while another shows redundant features with native ichthyofauna. We emphasize that the possible extinction of native species currently classified as threatened may lead to the disappearance of unique functional groups, which puts at risk the persistence and stability of these assemblages.

1. Introduction

Freshwater ichthyofaunas are currently facing a conservation crisis (Pelicice et al., 2017; Dudgeon, 2019). Recent studies have estimated that more than one-third of all freshwater fish species are on the brink of extinction (Hughes, 2021). Part of this threat is brought on by the presence of exotic species introduced by humans, which may end up replacing native species of local assemblages (Dudgeon et al., 2006; Vitule et al., 2019; Magalhães et al., 2021). The introduction of exotic species results in compositional changes, whose consequences for functional diversity represents a key- but poorly understood– aspect in a conservation context (Cadotte et al., 2011; Richardson et al., 2018; Magalhães et al., 2020; Souza et al., 2021; Su et al., 2021).

Functional diversity can be defined as the complete set of ecologically relevant traits that are present in a given assemblage (Mouillot

et al., 2013a; Leitão et al., 2016; Toussaint et al., 2018; Souza et al., 2021). Several components of functional diversity have been recognized, being defined on the assumption that the set of species that form a given assemblage also constitute a multidimensional functional trait space (Mouchet et al., 2010). This space can be characterized in terms of: (a) its multidimensional volume or functional richness (Villéger et al., 2008); (b) degree of separation shown by species within the confines of that space or functional divergence richness (Villéger et al., 2008); (c) mean distance between each species and its closest neighbor or functional originality (Mouillot et al., 2013a); and (d) mean distance between each species and the center of the functional space or specialization (Bellwood et al., 2006). Given that these functional diversity components are independent from each other, it is expected that their response to compositional changes in a given assemblage will also be independent, i.e., decoupled (Villéger et al., 2008). Therefore, the

quantification of these components represents a key challenge in understanding the effects that exotic species have on the functional diversity and stability of local assemblages (Mouchet et al., 2010; Souza et al., 2021).

Most studies analyzing the functional diversity of freshwater fish assemblages have focused on only one of these components: functional richness (FRic), without exploring changes in the other three. According to reported findings, the presence of exotic species increases the FRic of assemblages, because they usually possess novel functional traits that are absent locally (Toussaint et al., 2018; Souza et al., 2021). Additionally, the extinction of native species –which tend to show higher levels of FSpe in local assemblages–, causes FRic to decrease by the disappearance of functional traits from the multidimensional space (Mouillot et al., 2014; Leduc et al., 2015; Su et al., 2021). Thus, the effects of the introduction and subsequent extinction of species on the different functional diversity components will depend on the position that the new species occupy within the functional space of the assemblage, and on the functional diversity component of interest itself (Petchey and Gaston, 2002; Mori et al., 2013; Souza et al., 2021).

Over 75% of the total functional diversity of freshwater fishes is concentrated in the Neotropical region, thus considered a global conservation priority (Toussaint et al., 2016; Vitule et al., 2019). Within this region, the freshwater fish fauna of Chile presents low species richness ($S = 42$; Vila and Quezada-Romegialli, 2018), but a high degree of endemism (close to 77%; MMA, 2021). These compositional characteristics are the result of the long history of biogeographic isolation of the Chilean assemblages from the remainder of the Neotropics (Habit et al., 2006). Recent studies in Chile have verified that the introduction of 28 exotic species has increased both taxonomic and functional richness (FRic) of these assemblages (Rojas et al., 2020; Rojas et al., 2021). Nevertheless, it remains poorly understood how the other components of functional diversity (i.e.: divergence, specialization, and originality) have been affected.

In this article, we report how the four functional diversity components change in response to the introduction of exotic species. We analyze 20 freshwater fish assemblages from Chile, and assess changes in functional richness, divergence, specialization, and originality. Based on information on the distribution of both native and exotic species, and on the conservation status of native ones, we identify three compositional stages –historical, current, and future– for which we quantify the values of the different components of functional diversity. Because each of these components represents an independent measure of functional diversity, we hypothesize that following the introduction of exotic species into Chilean hydrographic basins, functional richness, divergence, specialization, and originality should show changes that are decoupled from each other.

2. Materials and methods

2.1. The study basins

Our study was carried out in 20 hydrographic basins in Chile, encompassing from the central to the southernmost zones of the country (Fig. 1). The water sources are in the high-Andean area and the waters flow into the Pacific Ocean in all of them. These basins cover a total area of 225,705 km^2 (DGA, 2020), which represents 30% of the continental national territory (IGM, 2020). Specifically, the basins studied were: Elqui, Limarí, Choapa, Aconcagua, Maipo, Rapel, Mataquito, Maule, Itata, Andalién, Bíobío, and Imperial, all of them belonging to the Chilean ichthyogeographical province (Fig. 1; Vila and Quezada-Romegialli, 2018); Toltén, Valdivia, Bueno, and Maullín belonging to the Valdivian Lakes province (Fig. 1; Vila and Quezada-Romegialli, 2018); and Palena, Cisnes, Aysén, and Baker from Patagonia province (Fig. 1; Vila and Quezada-Romegialli, 2018).
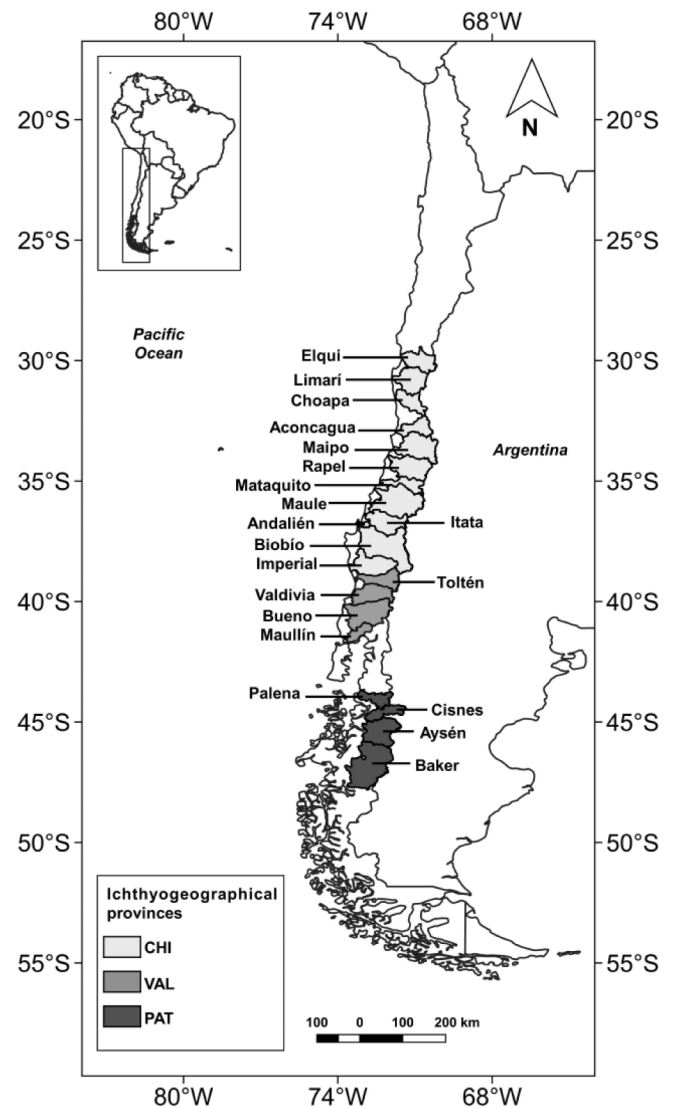

Fig. 1. Geographic location of the 20 hydrographic basins of interest in Chile. In gray shades the basins belonging to different ichthyogeographical provinces are shown: CHI: Chilean province; VAL: Valdivian Lakes province; and PAT: Patagonian province.

2.2. Composition and geographical distribution of fish

We determined the geographical distribution of native and exotic species within each basin (Rojas et al., 2019; Rojas et al., 2020). A total of 58 species was identified in the basins studied, of which 30 (51.7%) were native and 28 (48.3%) were exotic (see Supplementary Material 1). Based on this information, we determined the historical (i.e., past) composition of the assemblages (H), considering the current distribution of native species (Castro et al., 2020). It is important to note that historically, species have not been transferred between Chilean basins and the only species to be declared extinct is *Diplomystes chilensis*, which was thus included as "present" in historical assemblages (Castro et al., 2020).

After excluding that extinct native species and including the current distribution of exotic species, we obtained the current (i.e., contemporary) composition of the assemblages (C; Vila and Habit, 2015). Finally, based on the threat level faced by native species (MMA, 2021), we developed likely future composition (F) scenarios by simulating the extinction of taxa listed as "vulnerable" or "endangered" by the Ministry of the Environment of Chile (MMA, 2021; see Supplementary Material 1).

2.3. Functional traits and functional diversity

To quantify the various components of functional diversity, we reviewed the life history strategies and functional traits of native and exotic species distributed in our 20 basins of interest. Following Matsuzaki et al., (2013), we chose nine ecological traits: Maximum adult body length, body shape, dietary range, position in the water column, body covering, sensory structures (barbels), mandibular protractibility, fecundity (number of eggs per clutch), and type of migration (see Supplementary Material 1). The information on functional traits was obtained from scientific articles and FishBase (Froese and Pauly, 2018).

Based on the above, we quantified functional diversity using the indices of richness (FRic; Villéger et al., 2008), divergence (FDiv; Mouillot et al., 2013a), specialization (FSpe; Villéger et al., 2010), and originality (FOri; Mouillot et al., 2013a). Using Gower dissimilarity, an index applicable to discrete as well as continuous characters (Gower, 1971), we devised an interspecific distance matrix (see Supplementary Material 1). This matrix was used in a Principal Coordinates Analysis (PCoA) to identify independent PCoA axes, which represent composite functional traits that allow us to calculate the volume of the convex hull –here considered as Functional richness, FRic– in a multidimensional functional space (Cornwell et al., 2006). We used the first three PCoA axes (PCoA1, PCoA2 and PCoA3), because that is the minimum number of axes needed to describe a high-quality multidimensional functional space (Villéger et al., 2008) using mean squared deviation (Maire et al., 2015). Functional divergence (FDiv) was determined based on the relative distance of each species from the barycenter of the functional space (Mouillot et al., 2013a). Values close or equal to one indicate that most species are near the boundaries of the functional space, while values close to zero indicate that most species are positioned close to the center. Functional specialization (FSpe) was calculated as the mean Euclidean distance between each species and the mean position of all the species present in the assemblage; also known as the barycenter of the functional space (Bellwood et al., 2006). Functional originality (FOri) was quantified as the mean distance between each species and the species closest to it in the functional space (Mouillot et al., 2013a). The values of FSpe and FOri range from 0 to 1, those close to 1 indicating that the species present in the assemblage show higher degrees of specialization and/or originality (Villéger et al., 2010).

Functional diversity indices were calculated using the distribution matrix of each compositional stage; i.e., the historical (FRic-H, FDiv-H, FSpe-H, and FOri-H), current (FRic-C, FDiv-C, FSpe-C, and FOri-C), and future scenarios without threatened native species (FRic-F, FDiv-F, FSpe-F, and FOri-F). All functional diversity analyses were carried out using the FD package in R 3.6.1(Laliberté and Legendre, 2010; Laliberté et al., 2014), and the "quality_funct_space" and "multidimFD" functions (Mouillot et al., 2013b).

2.4. Statistical analysis

How functional diversity indices (FRic, FDiv, FSpe, and FOri) change across the three compositional stages, was analyzed through a Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson, 2005). PERMANOVA significance levels were evaluated through 9,999 permutations using a reduced model (Anderson, 2001) and the threshold was established at $P < 0.05$. A pairwise *post-hoc* test – Student's *t*-test for PERMANOVA – was used to detect significant differences between stages for each functional diversity index. These analyses were carried out using Primer 6 + PERMANOVA (Clarke and Gorley, 2006).

3. Results

Based on PCoA distributions, the functional spaces of the historical (the gray area in Fig. 2) and current assemblages (the area delimited by a continuous black line in Fig. 2) are partially overlapped, denoting functional redundancy between some exotic and native species.
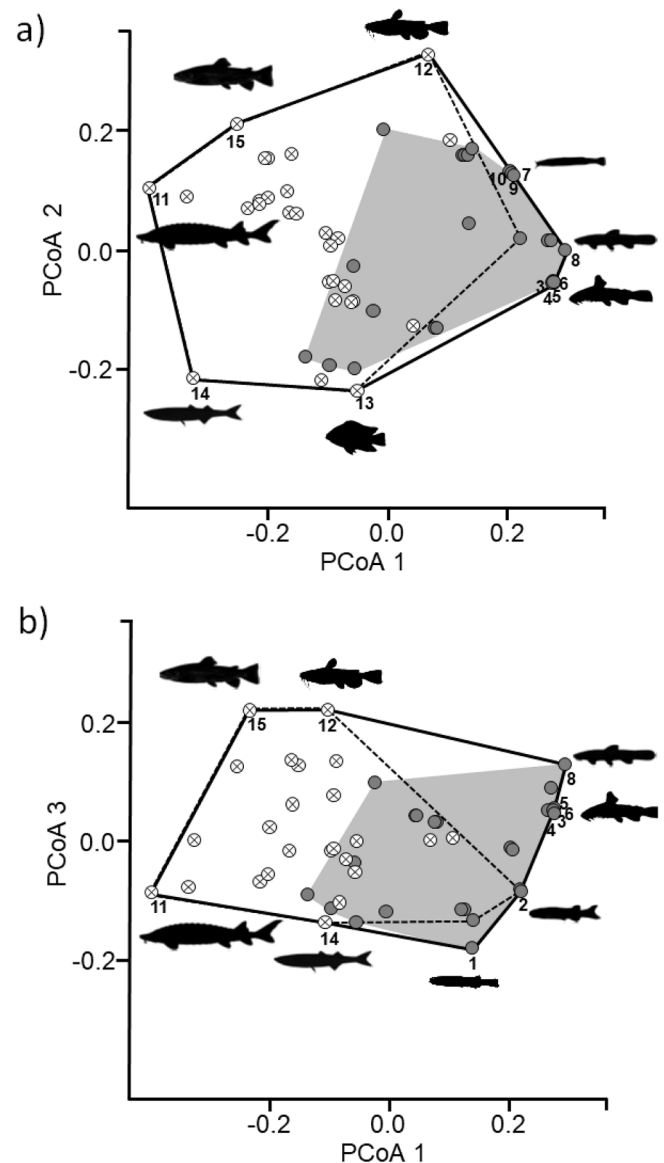
Fig. 2. Representation of the functional spaces of historical (gray area), current (area delimited by a continuous line) and future (area delimited by a segmented line) fish assemblages. Gray circles represent native species ($S = 30$) and circles with crosses represent exotic species ($S = 28$). Panel (a) represents axes PCoA1 and PCoA2; and panel (b) represents axes PCoA1 and PCoA3 of the functional space; species are plotted according to their traits. Numbers at vertices represent the coded species as follows; native species: (1) *Brachigalaxias bullocki*; (2) *Brachigalaxias gothei* (2) *Diplomystes camposensis*; (4) *Diplomystes chilensis*; (5) *Diplomystes incognitus*; (6) *Diplomystes nahuelbutaensis*; (7) *Hatcheria macraei*; (8) *Nematogenys inermis*; (9) *Trichomycterus areolatus*; (10) *Trichomycterus chiltoni*; and exotic species: (11) *Acipenser transmontanus*; (12) *Ameiurus melas*; (13) *Australoheros facetus*; (14) *Odontesthes bonariensis*; (15) *Salmo trutta*.

Nonetheless, a group of exotic species (*Acipenser transmontanus*, *Ameiurus melas*, *Australoheros facetus*, *Odontesthes bonariensis*, and *Salmo trutta*) increased the functional space of the current assemblage in comparison with the historical one (Fig. 2 A, B), especially along the PCoA1 axis. With the exception of *Australoheros facetus*, all those species present larger body length, broader dietary range, and higher fecundity, which were the most dissimilar traits between native and exotic ichthyofaunas (see Supplementary Material 1). On the other hand, a group of native species (*Diplomystes camposensis*, *Diplomystes incognitus*, *Diplomystes nahuelbutaensis*, *Hatcheria macraei*, *Nematogenys inermis*, *Trichomycterus areolatus*, and *Trichomycterus chiltoni*) showed unique traits,

not shared with exotic species (Fig. 2 A, B).

This group is characterized by the presence of sensory barbels that function in prey detection, dorsoventrally compressed body shape, demersal habits, and generally low fecundity (<500 eggs per reproductive event), which placed them in the peripheral regions of the functional space. The functional richness and functional originality showed a significant increase from historical to current assemblages (FRic-C > FRic-H; FOri-C > FOri-H, respectively; Fig. 3 a, d; Table 1), whereas functional divergence and functional specialization did not change significantly from historical to the present (Fig. 3 b, c; Table 1).

Under the future scenario –which considers the possible extinction of native species– the responses of functional diversity components were decoupled. When comparing between the historical and future assemblages, the following changes were observed: A small but statistically significant increase in FRic (FRic-F > FRic-H; Fig. 3a; Table 1), a significant reduction in FDiv (FDiv-F < FDiv-H; Fig. 3b; Table 1), and a significant increase in FOri (FOri-F > FOri-H; Fig. 3d; Table 1). FSpe did not change significantly between stages historical and future (Fig. 3C; Table 1). In the comparison of current and future assemblages, there was a significant reduction in FRic (FRic-C > FRic-F; Fig. 3a; Table 1) and FDiv (FDiv-C > FDiv-F; Fig. 3B; Table 1), and a significant increase in FOri (FOri-C < FOri-F Fig. 3d; Table 1). Again, no change was detected in FSpe (Fig. 3c; Table 1).

4. Discussion

Our analysis shows that the introduction of exotic species has caused

Table 1
Results of the Permutational Multivariate Analysis of Variance (PERMANOVA) followed by a pairwise *post-hoc* Student's *t*-test for PERMANOVA. Acronyms correspond to the indices of functional richness (FRic), divergence (FDiv), specialization (FSpe), and originality (FOri).

Main test	d.f.	MS	Pseudo-*F*	P(perm)
FRic	2	0.4	43.2	<0.001
FDiv	2	13.7	4.4	0.015
FSpe	2	6.3	0.3	0.755
FOri	2	0.1	100.9	<0.001
Pairwise tests	d.f.	*t*		P (MC)
FRic-H × FRic-C	1	85.1		<0.001
FRic-H × FRic-F	1	27.9		0.008
FRic-C × FRic-F	1	59.0		<0.001
FDiv-H × FDiv-C	1	0.9		0.334
FDiv-H × FDiv-F	1	31.0		0.005
FDiv-C × FDiv-F	1	20.2		0.050
FSpe-H × FSpe-C	1	0.7		0.494
FSpe-H × FSpe-F	1	534.1		0.958
FSpe-C × FSpe-F	1	0.6		0.540
FOri-H × FOri-C	1	70.6		<0.001
FOri-H × FOri-F	1	12.9		<0.001
FOri-C × FOri-F	1	78.2		<0.001

significant changes in the functional diversity of the freshwater fish assemblages in several ichthyofaunal provinces of Chile. The particular trend of change depends on the component analyzed (FRic, FDiv, FSpe, FOri), as well as the scenario (historical, current, and future composition). In Chilean basins, exotic species have increased FRic and FOri but
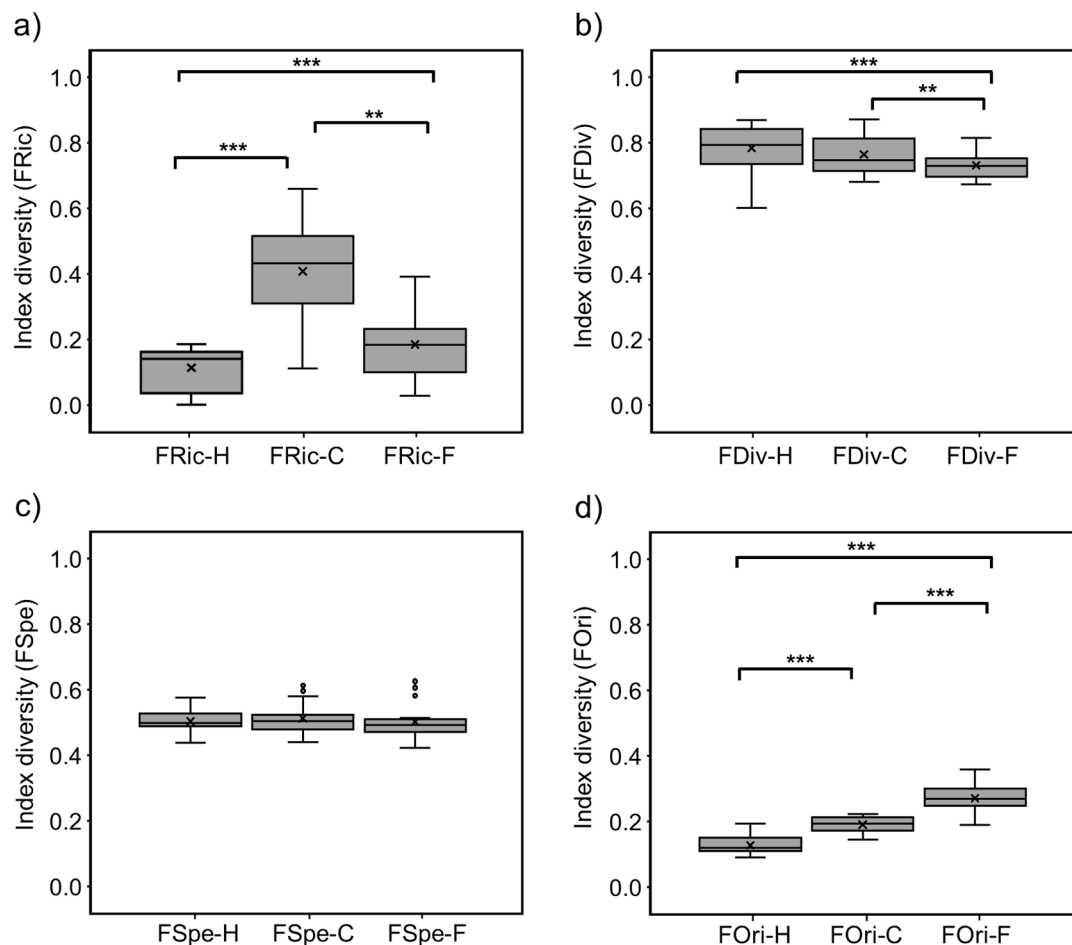
Fig. 3. Boxplot of functional diversity indices for historical (H), current (C), and future (F) assemblages: (a) functional richness (FRic); (b) functional divergence (FDiv); (c) functional specialization (FSpe); and (d) functional originality (FOri). The horizontal line and cross inside the boxes represent median and mean values, respectively. *P < 0.05; **P < 0.01; ***P < 0.001.

have not changed FDiv and FSpe (shift from historical to current stage) promoted by the reduced number of specialist species (Mouillot et al., 2013a, 2013b). Nevertheless, if the endangered and vulnerable native species were to become extinct/extirpated, FSpe would not be affected, while the FRic and FDiv of assemblages would decrease and FOri would increase (shift from current to future stage).

On average, the presence of exotic fish species in Chile has increased FRic in our assemblages by 263%, a similar value to that observed in other Neotropical freshwater fish assemblages (246%; Toussaint et al., 2018) as well as in other regions (Villéger et al., 2014; Toussaint et al., 2016; Toussaint et al., 2018). In Chile, this increase was mainly due to a subset of exotic species possessing novel functional traits that are absent in native assemblages. In this sense, exotic species such as *Acipenser transmontanus*, *Ameiurus melas*, *Australoheros facetus*, *Odontesthes bonariensis* and salmonids from the genera *Oncorhynchus* and *Salmo* show larger values in traits such as body length (>50 cm) and fecundity (>2,000 eggs, with the exception of *Australoheros facetus*) and a broader diet range (most are carnivores, which includes preying on other fish), placing them at the periphery of functional space (see Fig. 3). By contrast, native species such as *Cheirodon australe*, *Cheirodon galusdae*, *Cheirodon kiliani*, *Cheirodon pisciculus*, *Galaxias maculatus*, *Percilia gillissi*, and *Percilia irwini*]\ have smaller body length (<30 cm), lower fecundity, and a range of diet restricted to invertebrates (i.e., invertivores), making their location in functional space more central than exotic ones (Fig. 2). Among these functional traits, the piscivorous diet of some exotic species is particularly important, because it poses a threat to the conservation of native taxa (Soto et al., 2007; Penaluna et al., 2009; Correa et al., 2012; Elgueta et al., 2013; Habit et al., 2010; Habit et al., 2015).

The conservation status of 90% of all native species in Chile is under some degree of threat, caused by multiple stressors, particularly the introduction of exotic species, changes in soil use in the river basins, extraction of water, channeling of river systems and construction of hydropower plants (Vila and Habit 2015), which makes functional diversity analyses particularly relevant when examining the consequences of their eventual extirpation. Our findings predict a decrease in FRic to 59% of the current stage, brought on by the extinction of species and the resulting loss of unique functional traits –a pattern documented in other studies as well (Mouillot et al., 2013b; Pereira et al., 2021). In the case of Chile, several siluriform or catfish species in the families Diplomystidae, Nematogenyidae, and Trichomycteridae face the greatest risk of extirpation or extinction (all of them endemic to Chile, except for *Hatcheria macraei, Trichomycterus areolatus,* and *Olivaichthys viedmensis*; Supplementary Material 1). The family Diplomystidae are formed by taxa with traits that are considered primitive (Arratia, 2000), such as aspects of the maxillary bone, barbels, and low number of eggs (~300) (Lundberg et al., 2004; Vila et al., 1996), which means that their extinction would not only affect the functional diversity of the assemblages of Chile, but also those of the entire Neotropical region –because Siluriformes is the teleost order that contributes the most to global functional diversity (Toussaint et al., 2018; Souza et al., 2021).

We recorded significant changes in FDiv in Chile. In the 20 basins studied here, this index decreased significantly both in the H-F, and C-F stage shifts. This is in contrast with the results of other studies, which have reported that the presence of exotic species increases FDiv (Villéger et al., 2008; Toussaint et al., 2018). This is probably due to the persistence (lack of extinction) of native species, which show overlap with exotic species in functional space. Indeed, *Ameiurus nebulosus, Ictalurus punctatus, Jenynsia multidentata, Cnesterodon decemmaculatus, Cheirodon interruptus, Gambusia* spp., and *Cyprinus carpio* possess similar (i.e., redundant) functional traits to native species, such as smaller body length (<50 cm; with the exception of *Cyprinus carpio* and *Ictalurus punctatus*), mediolaterally compressed body shape, and a generalist diet consisting of invertebrates and plant matter (Supplementary Material 1). Therefore, these species occupy central positions in functional space, thus reducing FDiv through functional overlap with the native

ichthyofauna (Mouillot et al., 2013b). According to some authors, low FDiv could affect the stability of assemblages by intensifying interspecific competition (Lamothe et al., 2018). This mechanism may represent an additional threat to native species presence and their conservation (Habit et al., 2015).

In contrast to the results of other studies of Neotropical freshwater fish (Mouillot et al., 2014; Leitão et al., 2016), FOri increased significantly in the two compositional shifts (i.e., H-C and H-F). In the case of the current assemblages, this may be related to the presence of exotic species located at the margins of the functional space (Fig. 2), whereas in future assemblages it may be related to the loss of native species with traits shared by exotic ones (Fig. 3). For example, species in the siluriform genera *Diplomystes* (*Diplomystes camposensis, Diplomystes incognitus, Diplomystes nahuelbutaensis,* and *Olivaichthys viedmensis*) and *Nematogenys* (*Nematogenys inermis*) show high overlap in diet, which consists mostly of benthic invertebrates (Figueroa et al., 2010; Beltrán-Concha et al., 2012). Given that an increase in FOri can be interpreted as an indicator of decreased redundancy (Brandl et al., 2016; Chua et al., 2019), the disappearance of benthic species that feed on invertebrates may as well affect ecosystem processes and stability (Rosenfeld, 2002; Hooper et al., 2005).

The observed changes in functional diversity components in the fish assemblages of Chile are also linked to increased functional similarity (i. e., functional homogenization; Rojas et al., 2020; Rojas et al., 2021). As in studies carried out elsewhere in the Neotropics (Leitão et al., 2018; Daga et al., 2020; Magalhães et al., 2020), the presence of exotic species is causing functional homogenization (Su et al., 2021), which constitutes a risk for the stability and functional uniqueness of the assemblages studied (Rojas et al., 2020). Here, our results show that three of the four components of functional diversity analyzed here (FRic, FDiv, and FOri) favor the functional homogenization of the assemblages, while the fourth one (FSpe) does not change significantly, and therefore does not contribute to the functional homogenization.

Current Chilean conservation policies focus only on taxonomic aspects of assemblages, and few biotic management measures have been implemented beyond this level. As shown here, the functional facet of biodiversity also needs to be incorporated into environmental policies aiming to protect this unique and singular ichthyofauna. In this line, a particular effort - not contained in current Chilean legislation - requires establishing limitations on the anthropogenic expansion of exotic species already present in the territory. This provision could reduce the taxonomic and functional impact of exotic species on native species.

5. Conclusions

In conclusion, the freshwater fish assemblages of Chile show significant changes in the different components of functional diversity. Our results demonstrate that exotic species can be grouped into: (a) functionally redundant taxa, whose functional traits are shared with native species; and (b) functionally novel taxa, with traits that are not present in the native ichthyofauna. Therefore, the introduction of exotic species causes independent and/or decoupled changes in the different functional diversity components. Comparing current (or contemporary) with historical (or past) assemblages, FRic and FOri were found to have increased significantly, while FDiv declined, and FSpe was unaffected. In addition, we found that the extinction of native species may have similar effects on future assemblages, with the exception of FRic, which would likely decrease. Our findings highlight the importance of incorporating a functional aspect into diversity analyses of fish assemblages , through the study of its components of richness, specialization, divergence, and originality.

CRediT authorship contribution statement

Pablo Rojas: Conceptualization, Methodology, Software. **Sergio A. Castro:** Conceptualization, Methodology, Software. **Irma Vila:** Data

curation, Writing – original draft. **Fabian M. Jaksic:** Writing – original draft.

Declaration of Competing Interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi. org/10.1016/j.ecolind.2021.108364.

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