Pontificia Universidad Católica de Chile
Facultad de Ciencias Biológicas
Programa de Doctorado en Ciencias Biológicas
Mención Ecología

TESIS DOCTORAL:

MACROECOLOGY AND EVOLUTION OF MIGRATION IN FISHES

Por

DOMINIQUE ALÒ

Agosto 2019

Pontificia Universidad Católica de Chile
Facultad de Ciencias Biológicas
Programa de Doctorado en Ciencias Biológicas
Mención Ecología

TESIS DOCTORAL:

MACROECOLOGY AND EVOLUTION OF MIGRATION IN FISHES

Tesis presentada a la Pontificia Universidad Católica de Chile
como parte de los requisitos para optar al grado de
Doctor en Ciencias Biológicas mención Ecología

Por

DOMINIQUE ALÒ

Director de Tesis: Dr. Pablo Marquet I.

Comisión de Tesis: Dra. Evelyn Habit C.
                        Dr. Mauricio Lima A.
                        Dr. Eduardo Palma V.

Agosto 2019

AGRADECIMIENTOS

TABLE OF CONTENTS

RESUMEN

Las migraciones ocurren de forma recurrente en todo el reino animal y contribuyen a dar forma a la distribución actual de las especies en la Tierra. Todos los organismos muestran algún grado de transición de la residencia a la propensión a migrar y estas estrategias alternativas dependen de factores históricos y condiciones ambientales. En qué medida el comportamiento migratorio influye en la distribución actual de las especies y cuáles son los factores bióticos y abióticos que interactúan para dar forma a la riqueza y diversidad de las especies es un tema que todavía se está explorando. Existen diferentes estrategias asociadas con diferentes tipos de migración y los peces proporcionan un excelente sistema para estudiar y probar diferentes hipótesis dada su diversidad, distribución y variedad de tácticas migratorias. Este trabajo es una contribución a la exploración de diferentes facetas de la evolución y ecología de la migración en los peces. En particular, dada la hipótesis que los hábitats costeros en Chile son particularmente apto para sostener peces diadromos (que migran entre agua dulce y agua salada), en el primer capítulo de esta tesis doctoral utilicé la microquímica del otolito para documentar las diferentes historias de vida de peces nativos y exóticos, y discutí la importancia de la heterogeneidad del medio ambiente, junto con la propensión a la migración en la colonización de nuevos hábitats. El segundo capítulo está dedicado a la comprensión de la interacción de diferentes variables como la productividad ambiental, la energía, la heterogeneidad y/o la estructura filogenética para explicar la diversidad de los peces migratorios mediante análisis de vías. Los resultados sugieren que la riqueza actual de peces migratorios puede explicarse por la interacción de múltiples variables, pero estas variables interactúan de manera diferente en cada estrategia. Por ejemplo, la heterogeneidad ambiental es más importante en especies anádromas (es decir, las que crecen en agua salada y se reproducen en agua dulce). La propensión filogenética de determinados taxones a realizar migraciones y la dependencia de la anadromía en ambientes estacionales, sugiere que algunos peces migratorios pueden haber tenido distintos patrones de diversificación comparados a especies prevalentemente sedentarias. La hipótesis de la tasa de diversificación propone que a lo largo de la historia evolutiva, especies de linajes tropicales deberían tener tasas de diversificación mas altas. Dado que estudios recientes han cuestionado el apoyo a esta hipótesis, el tercer capítulo de esta tesis explora si la propensión al movimiento puede ayudar a explicar las diferencias en las tasas de especiación a través de la latitud y dados diferentes escenarios de historia de vida (residentes vs. migrantes). Los resultados corroboran que, en general, los peces muestran tasas de diversificación mas alta en latitudes mas bajas, pero también que las especies migratorias muestran patrones consistentes con tasas de diversificación más rápida en comparación a las especies residentes.

ABSTRACT

Migrations occur recurrently across the animal kingdom and contribute to shaping the current distribution of species on Earth. All organisms display some degree of transitions from residency to the propensity to migrate and these alternative strategies depend on historical constraints and environmental conditions. To which extent the migratory behavior influences current species distribution and which are the biotic and abiotic factors interacting to shape species richness and diversity is still a topic to be explored. There are different strategies associated with different types of migration and fishes provide an excellent system to study and test different hypotheses given their diversity, distribution, and variety of migratory tactics. This work is a contribution to exploring different facets of the evolution and ecology of migration in fishes. In particular, as coastal habitats in Chile are hypothesized to support a number of diadromous (migrate between fresh and saltwater) fish species, in the first chapter of this PhD thesis I used otolith microchemistry to document different life histories of native and exotic fishes, and discussed the role of heterogeneity of the environment coupled with migration propensity in promoting colonization of new habitats. The second chapter was dedicated to the understanding of the role and interaction of different variables such as environmental productivity, energy, heterogeneity, and/or phylogenetic structure in explaining the current diversity of migratory fishes using path analyses. Results suggest that migratory fish richness can be explained by the interaction of multiple variables, but these variables interact differentially in each strategy. For example, the role of environmental heterogeneity is strongest for anadromous (i.e. grow in saltwater and reproduce in freshwater) species. The phylogenetic propensity for selected taxa to undertake migrations and the dependence of anadromy on seasonal environments, suggests that some migrating fishes may have had a different diversification history. The diversification rate hypothesis posits that rates inferred from a phylogeny should be higher for species in tropical lineages. Given that recent studies have questioned support to this hypothesis, the third chapter of this thesis was set to explore whether the propensity to movement can help explain differences in speciation rates across latitude and given different life-history scenarios (residents versus migrants). Results show that, with some exceptions, migratory species display patterns of faster diversification rates compared to resident species and exhibit longer time periods between speciation events. Additionally, there is evidence that speciation rates are higher at lower latitudes as predicted from the diversification rate hypothesis. More research is needed to further deconstruct the different interacting roles of life-history, evolution, and ecology in shaping the distribution of life on Earth.

INTRODUCTION

The study of migrations has captivated human curiosity for a very long time, particularly due to some of the massive and spectacular migrations that can be observed in the animal kingdom. Migrations occur recurrently across the animal kingdom in all of its variations. From birds to mammals, insects, fish, reptiles, even zooplankton and humans, all display to some extent degrees of transitions from residency status to propensity to undertake migratory behavior (Dingle 2014). Whether or not a species, population or a segment within a population migrate can be based on several different factors. There are different strategies associated with different types of migration, for example, it can depend upon the age or sex of the individuals, it can be "obligate" or "facultative", it can be "differential" (i.e. members of the population follow different migration strategies) and "partial" (i.e. only part of the population migrates while the other remains sedentary as a special case of differential migration), "seasonal" or "irruptive"; it can also be "synchronized" and "predictable" by annual cycle, furthermore, there can be "one-way" migrations or "two-ways" migration (Table 1). For example many fish species undertake migrations that can be characterized by their function (spawning, refuge from predators, adverse environmental conditions, feeding), habitat, temporal scale at which they occur (seasonal, diel vertical or horizontal migration), and differential migration within individuals of the same population (alternative life-history strategies) (Alerstam et al. 2003; Börger et al. 2011; Brönmark et al. 2013). Although studies to define the "why", "when", and

"how" of migration are extensive, we still lack a unifying theory of migration toward which the first steps are just beginning to be taken (Dingle and Drake 2007; Milner-Gulland et al. 2011; Dingle 2014). Some of the most important contributions to the study of biology of migration are given in Table 2. Although, as the bibliography on the topic is very extensive, many important studies have been probably been left out. However, the literature cited in Table 2 should be able to catch the essence of the most relevant efforts built towards a comprehensive understanding of migrations in the animal kingdom. The following evolutionary and ecological elements are the most recurrent themes used to explain migrations: i) seasonality and heterogeneity of the habitat, ii) cost and benefit approach to fitness optimization, iii) genetic variation for phenotypic plasticity and traits specific for migration adaptations, iv) extinction avoidance.

Resource availability driven by both density-dependence mechanisms and seasonality of the environment can induce populations to migrate. Density-dependent habitat selection (Fretwell and Lucas 1969; Fretwell 1972) occurs when the fitness of individuals in one habitat depends on population growth. The population acts upon the environment and deteriorates the quality of the patch. Interesting data has shown density-dependence of locust migrations and how these insects can be driven elsewhere in collective motion both by competition and by the lack of resources (Buhl et al. 2006; Romanczuk et al. 2008; Simpson and Sword 2009; Yates et al. 2009). Early research on evolution of bird migrations suggested that migration is triggered by the existence of areas with seasonally favorable and unfavorable conditions. Migrations are a normal consequence of increased competition between and among species in seasonal environments (Cox 1968). Studies on arthropods observed that migrations should be

more likely to occur when species reside in temporary habitats, and that migration confers an evolutionary advantage to those species in need of adjusting to spatial and temporal habitat variation (Southwood 1962). Therefore, when species or populations occupy heterogeneous habitats, they may decide to shift their residence either temporarily (two-way migrations) or permanently (one-way migrations). Heterogeneity of habitat is ubiquitous and constantly changing, as even tropical habitats can display high degrees of seasonal variability in both climate and resource availability (Winemiller and Jepsen 1998); as a consequence, migrations are likely to occur anywhere and in any taxa, although in some areas and for some species their costs may be higher.

Lack (Lack 1954; Dingle 2014) was the first to apply a theoretical cost-benefit approach to the evolution of migration in birds, proposing that if the benefit-to-cost ratio of moving exceeds the ratio for staying, then migration should be favored by natural selection. Interestingly, the model has also been applied to model human migrations, as authors suggested that migration is a search for opportunities in higher-paying occupations and constitutes a response to "spatial earning differentials" (Sjaastad 1962; Borjas 1987). Fitness trade-offs in fishes have been analyzed by Gross (Gross 1987), as he recognized that migrations would occur when they are selectively advantageous over resident life histories. If the cost of staying as residents outweighs the benefits compared to the alternative environment, then, fish are better off leaving their original habitat for the new one, where they can get better resources and higher reproductive success. Very recently, migrations have also been shown (experimentally and with individual-based models (Railsback and Grimm 2012) to reflect fitness trade-offs in both crickets and locusts, as aggregations and constant

movement in one direction reduce costs due to competition for resources (Sword et al. 2005; Simpson et al. 2006).

Most of the physiological and morphological characteristics that may allow some taxa to show a higher propensity for long-distance migration should be under partial genetic control. As selection should favor genetically based mechanisms of dispersal, homing, or seasonal change in habitat preference if this leads to a reduction in total competition (theory developed for birds) (Cox 1968). Still, it has been argued, that animal migration is most likely to be a behavioral trait triggered by multiple ecological and environmental factors (Pulido 2011), as it has evolved repeatedly and very rapidly in many lineages. Therefore, it is interesting to discuss to what extent migratory behavior is dependent on phylogenetic inheritance or else an adaptive behavioral trait that remains latent in many animal taxa (Pulido 2007).

Several theories have highlighted how migration can evolve as a response to avoid extinction. For example, in birds, migration strategies are selected and maintained by natural selection through differential mortality, which is typically higher in residents (von Haartman 1968). For zooplankton, it has been suggested the "better hungry than dead" predator-avoidance theory (Lampert 1989), and studies on the evolution of flightlessness in insects have demonstrated how the probability of extinction decreases if a species migrates (Roff 1990). A few ancestral fish taxa are more likely to migrate than others (i.e. anguillid eels, lampreys) (McDowall 1997), and perhaps migration occurs most frequently in groups less able to solve problems of ecological isolation by morphological differentiation (Cox 1968).

The mechanisms mentioned offer generality to the study of migrations across phyla and my contributions will seek to address at least some aspects of the evolutionary and ecological perspectives listed above. Fishes offer an excellent system to study migrations because are part of a well-studied group of organisms, and large databases of taxonomic information, worldwide occurrences and life-history traits are freely available for researchers to access. Also, fishes have been categorized according to the medium in which they occur, offering easy access to study the effects of habitat changes on the distribution of different groups. As highlighted in Table 1, a unique and specific "migration terminology" has been designated just for fish (and some crustaceans) living at the interface between marine and freshwater environments, named *diadromy*, which describes the regular, predictable, physiologically mediated movements between freshwater and sea. Diadromy is usually obligatory for the majority of populations within a species, it can however trigger phenotypic differentiation, where some individuals stay as residents and others develop the migrating phenotype. Three different types of diadromy have been described, depending on the life history stages and zones at which each reproductive or feeding event occurs: *anadromy*, birth in freshwater (FW), growth in saltwater (SW), return to FW to reproduce; *catadromy*, birth in SW, growth in FW, return to SW to reproduce; *amphidromy*, growth and reproduction in FW, larval migration to SW, return to FW as juveniles (Myers 1949; McDowall 1988) (refer to Fig. 3 for a visual aid). The argument that justifies the warranting of a special nomenclature just for fishes capable of adapting to such fluctuations is that the boundary between freshwater and saltwater creates an unsurpassable osmotic barrier. Nevertheless, the literature presents several examples in many taxa, in which migration from one habitat to the next must also face

extreme environments and associated physiological and adaptive changes that could be comparable to the extreme osmoregulatory fluctuations encountered by diadromous fishes (e.g. hypoxia in birds, copepods, and krill; hypercapnia in blue crabs) (Ekau et al. 2010; Stover et al. 2013; Altshuler et al. 2016). Additional categorizations of migration in fishes include *oceanodromy* and *potamodromy*. The first strategy describes fishes that migrate exclusively within the saltwater medium whereas potamodromous fishes are those identified as exclusive freshwater migrants (see Northcote, 1997 for a review on potamodromous strategies).

It has been difficult to define the factors the may contribute to the occurrence of migrations in fishes because of confounding aspects such as uneven geographic and phylogenetic distribution. For example, sea-migration in anadromous species can be more common at high latitudes, whereas populations inhabiting lower latitudes are more often just confined to freshwater; in fact, it has been shown that when non-anadromous, lower latitude stocks are transplanted north of 65°N transplanted fish can become anadromous during their lifetime (Nordeng 1983; McDowall 1988). It is also interesting to note that among the 47 native continental fish species currently recognized in Chile (this number includes marine fishes that may infiltrate in freshwater), 30% exhibit some degree of plasticity shifting between saline and freshwater habitats, and 15% have already been suggested to display diadromous behaviour (Alò et al. 2019), compared to just 1% of world fishes (Nelson 2006a); further remarking that most of these species belong exclusively to two families and occur South of 39° of latitude.

Several questions arise from these observations, such as "Why do some fishes decide to migrate, submitting themselves to drastic environmental changes, facing the high costs of

coping with predation risks and often with the physiological changes associated with salinity fluctuations? And yet, why are some species more likely to migrate than others?

To explain the phenomenon, different hypotheses have been proposed, among which phylogeny, habitat productivity, optimization of reproductive effort, or triggers driven by stressful conditions as some of the agents proposed to be directly responsible for the current distribution of migratory fish species (Gross 1987; Gross et al. 1988; McDowall 1988; Tsukamoto et al. 2009). However the argument is still open for discussion, possibly because the study of migration in fishes has traditionally been kept isolated from the study of migration in other taxa.

My research is devoted to the study of the evolution and ecology of migration in fishes, trying to fill knowledge gaps, re-test older predictions based on the availability of new and more complete datasets, and testing several of the hypotheses proposed in the past to study migrations. This work is comprised of three chapters which are organized independently as they analyze patterns of fish migrations from different angles: i) a strictly empirical, local, and field component with direct implications for conservation in Chile, where otolith microchemistry was used to detect migratory habits in native galaxiids and exotic salmonids in Patagonia; ii) a macroecological perspective of fish migrations, which examines spatial patterns of distribution and seeks to define whether different migratory life-histories can be directly related to environmental variables such as temperature and productivity and historical legacies dictated by phylogenetic diversity; iii) an evolutionary analysis using comparative phylogenetics, where the goal is to detect a distinctive evolutionary signal in migratory fishes

by measuring their phylogenetic distinctiveness and speciation rates using a comparative approach with data obtained from the most recent fish backbone phylogeny.

1. CHAPTER ONE: Otolith microchemistry and diadromy in Patagonian river fishes

Authors: Dominique Alò[1, 2], Cristian Correa[3], Horacio Samaniego[2], Corey A. Krabbenhoft[4, 5], Thomas F. Turner[4]

[1]Departamento de Ecología, Pontificia Universidad Católica de Chile, Santiago, Chile

[2]Laboratorio de Ecoinformática, Universidad Austral de Chile, Valdivia, Los Ríos, Chile

[3]Instituto de Conservación Biodiversidad y Territorio, Universidad Austral de Chile, Valdivia, Los Ríos, Chile

[4]Department of Biology and Museum of Southwestern Biology, University of New Mexico, Albuquerque, New Mexico, U.S.A

[5]present address: Department of Biological Sciences, Wayne State University, Detroit, Michigan, U.S.A.

Corresponding Author:

Dominique Alò

Email address: dominiquealo@gmail.com

1.1. ABSTRACT

Coastal habitats in Chile are hypothesized to support a number of diadromous fish species. The objective of this study was to document migratory life histories of native galaxiids and introduced salmonids from a wide latitudinal range in Chilean Patagonia (39-48°S). Otolith microchemistry data were analysed using a recursive partitioning approach to test for diadromy. Based on annular analysis of Sr:Ca ratios, a diadromous life history was suggested for populations of native *Aplochiton taeniatus*, *A. marinus*, and *Galaxias maculatus*. Lifetime residency in freshwater was suggested for populations of *A. zebra* and *G. platei*. Among introduced salmonids, populations of *Oncorhynchus tshawytscha* and *O. kisutch* exhibited patterns consistent with anadromy, whereas the screened population of *O. mykiss* appeared restricted to freshwater. *Salmo trutta* exhibited variable patterns suggesting freshwater residency and possibly anadromy in one case. The capacity and geographic scope of hydropower development is increasing and may disrupt migratory routes of diadromous fishes. Identification of diadromous species is a critical first step for preventing their loss due to hydropower development.

1.2. INTRODUCTION

Only 47 native and 27 non-native inland fish species are currently recognized in Chile, and several of these are thought to exhibit some tolerance for shifting between saline and freshwater habitats (Dyer 2000; Habit and Victoriano 2005; Habit et al. 2006; Vila et al. 2011; Ministerio del Medio Ambiente 2013; Vargas et al. 2015). Approximately 15% of these fishes are hypothesized to display diadromous migratory behaviour (Table S1), compared to less than 1% for fishes worldwide (Nelson 2006b).

The term diadromy describes regular, predictable, and physiologically mediated movements between freshwater and the sea. Diadromy necessitates profound physiological changes (i.e., osmoregulation) when shifting from marine to freshwater habitats and vice versa (Gross et al. 1988). Diadromy can be either obligatory or facultative (Dingle and Drake 2007). The direction of migration depends on life history stages and habitats where reproductive and feeding events occur. The combination of these factors defines three different types of diadromy: anadromy, catadromy, and amphidromy (Myers 1949; Gross 1987; Gross et al. 1988; McDowall 1992; McDowall 1997; Limburg et al. 2001) (in particular refer to McDowall 1997 for a review of the terminology and a visual aid).

Given the high percentage of fishes in Chile hypothesized to exhibit some form of diadromy, migration might play an important, yet unrecognized role in establishing national

priorities of aquatic biodiversity conservation. At present, a high percentage of the continental ichthyofauna in Chile is categorized with some degree of conservation threat by Chilean environmental agencies and other authors, although conservation categories can be incongruent and threats underestimated (Habit and Victoriano 2005; Diario Oficial de la Republica de Chile 2008; Ministerio del Medio Ambiente 2013; IUCN 2015; Vargas et al. 2015).

Coastal habitats in Chile appear well suited to support establishment of diadromous species. Andean rivers that flow into the Pacific Ocean include a variety of different habitats in a limited longitudinal distance (average 145 km), spanning from areas of rocky substrates, high elevation gradients, clear waters and low temperatures, to areas of low flow, sandy substrates, and aquatic vegetation (Habit and Victoriano 2005; Instituto Nacional de Estadisticas 2015). Spatial habitat heterogeneity is essential for maintenance and completion of diadromous life cycles, and for maintaining evolutionary potential (i.e., genetic diversity) for life history variation (Pulido 2007; Dingle 2014). Therefore, fragmentation events imposed by human-made barriers may affect fish fitness and restrict movement between habitats more so than in other areas (Waples et al. 2007).

Patagonian fishes offer a unique opportunity to understand migration patterns in relatively pristine habitats and establish a baseline against which future potential impacts associated with river impoundments can be compared. Despite strong economic growth and efforts to develop hydroelectric potential to meet the country's growing energetic demand (Joo et al. 2015), many rivers in southern Chile are still free-flowing, offering opportunities to study pre-impoundment patterns of diadromous migration. In particular, galaxiid fishes are

distributed across the temperate Southern Hemisphere (McDowall 2002a) and diadromy seems to be a recurrent trait among many of the species (McDowall 1971; McDowall 1988). Likewise, salmonids are among some of the best studied diadromous fishes in the Northern Hemisphere and are now well established in southern Chile (McDowall 2002b; Correa and Gross 2008).

Using micro-geochemical data obtained from otoliths, this study sought to investigate whether native galaxiids and introduced salmonids exhibit diadromy in Chilean rivers. Otoliths are calcified deposits in the inner ear of fishes that accumulate in ring-like fashion over ontogenetic growth. Elemental analysis of otoliths can help to distinguish origins of marine and freshwater fishes among locations with variable water chemistry. Differing chemical composition of the otolith from the primordium (core) to the edge is indicative of the different environments in which a fish has lived and allows for hypothesis tests related to patterns of fish movement. When analysed sequentially across an otolith sagittal section, changes in elemental ratios can inform fine-scale patterns of movement, connectivity, dispersal, and the location of natal habitats (Halden et al. 2000; Howland et al. 2001; Kraus 2004; Ashford et al. 2005; Campana 2005; Arkhipkin et al. 2009). To quantify these changes in Patagonian fishes, we applied univariate recursive partitioning approaches based on Classification and Regression Trees (CART) to detect discontinuities in elemental ratios that may indicate habitat shifts (Vignon 2015).

This research was motivated by the necessity to understand the potential for movement in native and exotic fishes in non-impounded systems in southern Chile and used an existing sample pool (Correa et al. 2012; Correa and Hendry 2012a; Correa and Hendry 2012b; Alò et

al. 2013). Several native fishes have previously been hypothesised to exhibit capacity for shifting between marine and freshwater habitats (Dyer 2000; Habit and Victoriano 2005; Habit et al. 2006; Vila et al. 2011; Ministerio del Medio Ambiente 2013; Górski et al. 2015; Vargas et al. 2015) and some exotic salmonids appear to have established successful diadromous life-histories (Ciancio et al. 2005; Riva-Rossi et al. 2007; Ciancio et al. 2008; Correa and Gross 2008; Arismendi and Soto 2012; Araya et al. 2014; Górski et al. 2016). This study sought to characterize the potential diadromous characteristics from a wider diversity of native and exotic fish species in Patagonia, including previously unevaluated species sampled from a wider and unexplored geographic range. Inclusion of native and exotic species in this study provided a framework to compare well-known life-history characteristics of northern hemisphere salmonids to the lesser-known galaxiids.

1.3. METHODS

1.3.1. Fish Collections

Between 2004 and 2011, specimens of *Aplochiton zebra, A. taeniatus, A. marinus, Galaxias maculatus*, *G. platei, Oncorynchus tshawytscha, O. kisutch, O. mykiss,* and *Salmo trutta* were collected using various methods from six locations across a large latitudinal range (39.5–48.0° S) in western Patagonia, Chile (Fig. 2, Table 3). At each location, fish specimens were euthanized by an overdose of anaesthetic solution (tricaine-methanesulfonate MS-222 or clove oil). Due to the difficulties in morphological identification, genetic data were used to identify individuals in the genus *Aplochiton* to the species level (Alò et al. 2013). The McGill University Animal Care Committee (UACC), Animal Use Protocol No. 5291, approved use and handling of animals.

1.3.2. Otolith preparation

This study used the Strontium (Sr) to Calcium (Ca) molar ratio to infer habitat shifts across salinity gradients of Patagonian fishes. Strontium is particularly useful for reconstructing environmental history of fishes as it replaces Ca in the otolith matrix according to its availability in the fish habitat (Secor and Rooker 2000; Campana 2005; Pracheil et al. 2014).

Prior to specimen preservation, sagittal otoliths were extracted and either stored dry in

test tubes or in 95% ethanol, as elemental compositions and structures of otoliths are not strongly affected by ethanol for the elements assayed (Proctor and Thresher 1998).

In the laboratory, otoliths were polished, cleaned, and mounted individually on clean glass slides using a thermoplastic cement (Crystalbond™). In order to expose growth rings, 3M™ (fine) and Nanolap ® Technologies (coarse) diamond lapping film wetted with deionized water was used to polish otoliths by hand until a satisfactory sagittal section of annuli was visible (Fowler et al. 1995). For *Aplochiton* spp.*, Galaxias* spp.*, S. trutta, O. kisutch* and *O. mykiss* otoliths, a 30-μm and then 3-μm lapping film was used to expose annuli and get a finished polish. *O. tshawytscha* otoliths required larger lapping film (45 and 60 μm) to reach an appropriate view, but were finished with 3 μm film for increased clarity. For larger otoliths (e.g., *O. tshawytscha*), it was sometimes necessary to polish on opposite sides to produce a thinner section.

Following polishing, the mounting adhesive was dissolved in a 100% acetone bath and sonicated for 10 minutes. Larger otoliths were cleaned a second time with acetone as needed. Each otolith was then sonicated twice in Milli-Q water for 5 to 10 minutes each. Following cleaning, otoliths were rinsed a final time in Milli-Q water, transferred to clean vials and placed in a positive laminar flow hood for 24-48 hours to dry (similar to methods of Elsdon & Gillanders, 2002).

Acid-washed porcelain forceps were used to mount clean, dry otoliths on acid-washed microscope slides. Otoliths were grouped according to diameter and mounted 10-28 per slide accordingly. Each otolith was placed within one small drop of fresh Crystalbond melted onto a single slide.

Slides were securely kept in acid-washed, sealed petri dishes for transport to Woods Hole Oceanographic Institute (Woods Hole, MA, U.S.A.). There, Laser ablation-inductively coupled plasma-mass spectrometry (LA-ICP-MS) was conducted from October 8th to 11th, 2012 (*Aplochiton* spp*., S. trutta, Galaxias* spp*., O. kisutch,* and *O. mykiss*) and again from February 4th to 5th, 2013 (*O. tshawytscha*). Laser ablation was performed with a large format laser ablation cell on a New Wave UP193 (Electro Scientific Industries, Portland, Oregon) short pulse width excimer laser ablation system. This was coupled with a Thermo Finnigan Element2 sector field argon plasma spectrometer (Thermo Electron Corporation, Bremen, Germany) for elemental analysis. The laser was configured for single pass, straight line scanning at a speed of 5 µm per second. The laser beam spot size was 50 µm at 75% intensity and 10 Hz pulse rate. Isotopic activity rates (counts per second) were determined for ^{87}Sr and ^{47}Ca. Certified standard FEBS-1 (Sturgeon et al. 2005) and a 1% nitric acid (HNO_3) blank were passed through the instrument before and after each block of 4 to 11 otoliths to minimize bias in elemental mass. Each otolith was visualized on screen and the intended ablation transect of each sample was plotted digitally and analysed by ablation with a laser beam (refer to Fig. 3 or supplemental pictures: https://figshare.com/s/9855cff84b6b085f1b34 for a visual example).

1.3.3. *Data Analysis*

Digital images of each otolith were taken after the laser ablation procedure with a digital Nikon Coolpix P6000 split with a Martin microscope MM Cool mounted on Nikon SMZ800

lenses and illuminated with a NII-LED High Intensity Illuminator (Supplemental pictures: https://figshare.com/s/9855cff84b6b085f1b34).

For accuracy, each raw data point was produced from an average of ten consecutive reads. Isotopic intensities were corrected subtracting the means of the isotopic intensities detected in the blanks. Points below the limit of detection of the same isotope measured in the blanks (mean - 3SD) were eliminated. Isotopic intensities were converted to elemental intensities by taking into account the percent natural occurrence of the isotopes. Strontium was standardized to Ca and converted to molar Sr:Ca ratios using sequentially the measurements of the standard reference material, and the atomic mass of the elements analysed (Wells et al. 2003; Wolff et al. 2013). Elemental data and otolith transects were rigorously checked, and outliers caused by recording errors were removed (additive outliers, R Package "tsoutliers" v: 0.6–5, L'opez-de-Lacalle 2016). The ideal double life-history transect obtained ran across each sagittal otolith and through the primordium, thus providing two similar (redundant) patterns related to life history variation, one on either side of the primordium. Interpretations were based on the analyses of both sides of each double transect, if possible. However, in a number of cases, transects were imperfect due to damaged otoliths or inaccurate ablation pathways (Supplemental pictures: https://figshare.com/s/9855cff84b6b085f1b34). In these cases, data were analysed as partial transects that were used to differentiate putatively diadromous or resident signals (Fig. 3).

Classification and Regression Trees (CART, Breiman et al. 1984) were used to detect shifts in elemental ratios across the otolith transect. CART is an alternative to qualitative methods traditionally used to interpret the chronological signal in otolith microchemistry

transects (Vignon 2015). The position along the otolith transect (predictor variable) was recursively partitioned using regression trees in order to differentiate segments of the transect that shared similar mean Sr:Ca values (response variables) (Breiman et al. 1984; Therneau and Atkinson 1997; De'ath 2002; Strobl 2009). CART was implemented in the Tampo library (version 1.0) for R Statistical Software 3.0.2 (Vignon 2015).

Summary statistics of molar Sr:Ca ratios were calculated across all individuals. The main goal of this work was to represent movement patterns at a broad scale. Therefore, since shifts in Sr:Ca have been well documented in many species of fish moving across environments with variable Sr (Tzeng and Tsai 1994; Limburg 1995; Tzeng et al. 1997; Campana 1999; Limburg et al. 2001; Chang et al. 2004; Araya et al. 2014), CART analysis was used in a semi-supervised manner to identify the presence or absence of sudden discontinuities in the Sr:Ca otolith signal (Vignon 2015). This was done by setting three progressively relaxed conditions to the splitting procedure. A splitting condition is the minimum difference in mean values between consecutive Sr:Ca profile segments beyond which the segments are permanently split in different categories. The three splitting conditions adopted were 0.5, 0.7, and 1.0. The detection of one or more discontinuities or splits in the Sr:Ca signal was interpreted as evidence in favour of diadromy, or otherwise, evidence in favour of residency. When diadromy was inferred, the direction of ontogenetic movements was deduced from differences in segment means; increasing values indicated movements towards the sea, and vice versa.

Further inference about habitat occupancy (freshwaters, estuaries, or the sea) required a visual, heuristic examination of Sr:Ca profiles in relation to i) the sites of capture, ii)

comparisons with movement patterns inferred from all the species analysed, iii) assumption of positive correlation between environmental Sr and marine influence (Secor and Rooker 2000). Finally, all evidence was assembled to make individual inferences about migration patterns suggestive of amphidromy, catadromy, or anadromy. However, determining the precise extent of movements between habitats was beyond the scope of this work. Finally, otolith transect quality affected the confidence of our interpretations; from maximum confidence on inferences from transects that conformed to the hypotheses of the models proposed in Fig. 3, to uncertain interpretations from incomplete or faulty transects.

1.4. RESULTS

Observed variation in Sr:Ca ratios (Fig. 4) reflected a wide gradient of average values (lowest

mean (sd) 0.66 (+/-0.088) in *G. platei* and highest mean 4.03 (+/- 1.54) in *G. maculatus*).

Depending on the species or population analysed, CART identified patterns of change in Sr:Ca

elemental ratios consistent with different migratory life histories proposed in the schematic

representation in Fig. 3. Representative individuals for each species are shown in Fig. 5.

Details on the splitting results of all individuals under different stringency conditions are given

in Fig. 6. A summary of the inferred migratory strategy for each species is shown in Table 3.

1.4.1. Native galaxiids.

Large elemental shifts in otolith profiles suggested a catadromous life-history for most *A.*

taeniatus analysed (Table 3 and Fig. 6). Even when confined to strictly freshwater habitats, as

in Lake Caro, *A. taeniatus* juveniles showed a mild shift in Sr:Ca suggesting movements

between freshwater habitats (Fig. 6, cond.= 0.5), as contrasted with *A. zebra* or *O. mykiss*,

which showed no such shifts.

Otolith profiles (Fig. 5 and 6) suggested that *A. marinus* copes with high levels of

salinity variation in the Baker River system. Otolith primordia of all specimens of *A. marinus*

showed evidence of higher Sr:Ca ratios at early stages of growth, presumably before the fish

entered the estuary (site of capture). Taken together, these data suggest that *A. marinus* is catadromous.

Results indicated that *A. zebra* uses a chemically uniform habitat at both collection localities (Fig. 5), although results should be corroborated by future studies because *A. zebra* individuals assayed were juveniles. Nevertheless, specimens from Tocoihue River appear to have been exposed to marine influence compared to those from Lake Caro, suggesting preference for freshwater residency, but capacity for osmoregulation when salinity levels increase.

G. maculatus individuals were sampled from the same site as some specimens of *A. zebra* (Tocoihue). However, among four specimens assayed, three showed the highest variation in Sr:Ca compared to any other galaxiid species analysed (Fig. 4) with evidence of both catadromous and amphidromous transitions (Table 3). The *G. maculatus* specimen in Fig. 5 was caught in the lower reach of the Tocoihue River in an area with strong tidal influence. The otolith profile suggests an amphidromous life-cycle with intermediate Sr:Ca levels in the primordium followed by increases in Sr:Ca ratio and subsequent decrease to lower Sr:Ca levels. A fourth specimen of *G. maculatus* showed no major Sr:Ca fluctuations across the otolith transect, suggesting that this individual did not drift out to the ocean during its larval stage.

Only one specimen from the low-elevation coastal Palos Lake was assayed for *G. platei*, and results indicate freshwater residency as revealed by uniformly low Sr:Ca ratios across the entire otolith transect (Fig. 4 and 5).

1.4.2. Introduced salmonids

This study supports established anadromy in *O. tshawytscha* in Patagonia, as previously shown by other authors (Ciancio et al. 2005; Correa and Gross 2008; Arismendi and Soto 2012; Araya et al. 2014). Data are consistent with changes in Sr:Ca concentration levels that suggest hatching in freshwater, migration to areas with marine influence followed by a return to inland, freshwater areas to spawn (Fig. 5). *O. tshawytscha* specimens collected from the Simpson River do not show as much variation as other *O. tshawytscha* from this study most likely because these fish were all juveniles that had not yet migrated.

The two parr *O. kisutch* analysed revealed one substantial Sr:Ca shift between birth and time of capture. Both otolith profiles showed relatively high Sr:Ca signatures around the core that diminished substantially towards the edges (Fig. 5). These specimens where caught during the summer, about 55 km upstream of the Baker River's mainstream. The observed pattern is consistent with maternal effects imprinting a marine signature near the core, which is formed during the yolk absorption phase (Kalish 1990; Volk et al. 2000; Zimmerman and Reeves 2002). Our results add to the sparse documentation of the establishment of self-sustaining *O. kisutch* populations in southern Patagonia (Górski et al. 2016). Conversely, *O. mykiss* exhibited a pattern consistent with freshwater residency and minor Sr:Ca fluctuations over the entire life cycle (Fig. 4 and 6).

Evidence of at least two different life cycle patterns emerged for *S. trutta* specimens caught at three different locations. The Sr:Ca transect of juveniles from Lake Caro and adults from Lake Palos showed a pattern consistent with continuous residency in freshwater (Fig. 4 and 6) whereas *S. trutta* from Baker River showed higher values at the primordium (Fig. 5).

1.5. DISCUSSION

This study quantitatively identified significant transitions across otolith profiles using regression trees on Sr:Ca ratios. Native galaxiids showed considerable variation in putative habitat shifts when compared across species, with some species exhibiting differences at the population and individual levels, indicating a high degree of plasticity. Of five native galaxiids examined, evidence was found for one catadromous (*A. marinus*) and two facultatively amphidromous or catadromous species (*G. maculatus* and *A. taeniatus*). Nonnative salmonids have established populations with a broad array of migratory life histories, reflective of those found in their native ranges. Patterns consistent with anadromy were present in three (*O. tshawytscha, O. kisutch, S. trutta*) of four species included in this study.

Several species appear to regularly use habitats with different levels of marine influence. Otolith profiles that showed variation under the most restrictive analytical conditions were those most likely to exhibit large-scale habitat shifts between different environments and salinity levels (*A. taeniatus, A. marinus, G. maculatus, O. tshawytscha*). Otolith profiles that varied under less stringent conditions hinted at subtler shifts within habitat types.

Results suggest a preponderance of euryhaline (i.e. broad tolerance to different salinity levels) and facultative diadromous species among native galaxiids and introduced salmonids in Patagonia. The inferences on species migratory status by population, reported in Table 3,

suggest that some species display a diverse range of life history strategies (facultative diadromy), coinciding with an increasing number of studies reporting flexibility in diadromous patterns for several fishes (Hicks et al. 2010; Augspurger et al. 2015; Górski et al. 2015). These studies included Southern Hemisphere fishes and revealed the variability of resident/migratory life histories within species. This work reinforces the shift from the classical view that tended to categorize species as exclusively resident or migratory

Otolith microchemistry for introduced salmonids suggested that some species have established movement strategies similar to those in their native ranges. The successful establishment of anadromous exotic salmonids in Chile reinforces the hypothesis that the biotic and abiotic conditions required for diadromy to be maintained (Gross et al. 1988) are present in Chilean waters.

Current knowledge of preferred habitats and common life-histories in native continental fishes of Chile indicates that approximately 30% of the species have a broad halohabitat distribution, including species adapted to life in saltpans, estuaries and a variety of different diadromous strategies (Table S1). On the other hand, only about 9% of fishes around the world are considered euryhaline and just a few display some form of diadromous migrations (Nelson 2006b; Schultz and McCormick 2013). Estuaries of temperate regions often stimulate the evolution of adaptation from seawater to freshwater and can be seen as hotspots for transitions (i.e. regions with a high number of species with propensity for movement between saltwater and freshwater) (Schultz and McCormick 2013; Ruiz-Jarabo et al. 2016).

The likelihood of freshwater colonization is affected by multiple factors. Colonization probability increases when habitats are disturbed by extreme events like glaciation, drought, volcanic and anthropogenic activities. Extreme events can leave freshwater habitats with low levels of biodiversity and prone to infiltration and acclimation from migratory or coastal euryhaline fishes. Habitats with wide temporal or spatial ranges in salinity also provide good hotspots for transitions because the acclimation response depends on the physiology of the fish and the timescale of fluctuations. Lower temperatures are prevalent at mid latitudes and these conditions favor higher rates of colonization, since salinity and temperature interact to affect energetic demands, ion uptake rate and membrane permeability of fishes (Greenwood, 1975 as cited in Bamber & Henderson, 1988, McDowall, 1988; Lee & Bell, 1999; Schultz & McCormick, 2013).

Specific physiological adaptations can also facilitate freshwater colonization propensity in fishes. For example, specialized gills allow movement between saltwater and freshwater (Lee and Bell 1999; Schultz and McCormick 2013) (i.e. atherinids). Further, certain groups of diadromous fishes (e.g. galaxiids, salmonids) demonstrate plasticity in osmoregulation. Diadromous species migrate between saltwater and freshwater habitats at different stages of their life-cycles, but as shown in this study, some switch to a resident strategy. Euryhalinity and diadromy can therefore be seen as key innovations that enable lineages to radiate into new environments (Bamber and Henderson 1988; Lee and Bell 1999; McDowall 2001; Schultz and McCormick 2013).

Diadromous migrations mostly promote gene flow among populations, but can also lead to landlocking, isolation and cladogenesis (McDowall 2001). Habitat characteristics of

coastal zones composed of estuaries separated by long stretches of open shore, may facilitate isolation and landlocking of diadromous and euryhaline fishes into more stable habitats. For example, very high within-species genetic diversity was found in *G. maculatus* across its New Zealand range and along most of the Chilean coast except between 30°S and 42°S in Chile, where *G. maculatus* displayed lower genetic diversity and higher levels of genetic structure (Lee and Bell 1999; Waters et al. 2000; González-Wevar et al. 2015). Higher levels of genetic structure found within populations of *G. maculatus* in Chile were hypothesized to depend on glaciation history, but variation in coastal configurations and oceanographic regimes can also be linked to population differentiation and isolation.

Comparative otolith microchemistry analysis suggested that fishes of southern Chile may require a heterogeneous and spatially connected environment to complete their life-cycles. These temperate areas may be considered a favourable environment for the development and maintenance of migratory strategies in fishes (i.e. galaxiids) and could provide useful tools to evaluate the influence of habitat discontinuities and biogeography on the spatial distribution, colonization rates and genetic diversity of euryhaline and diadromous fishes alike (i.e. atherinids, galaxiids, salmonids). Examining recent freshwater invasions can yield insights into the osmoregulatory systems that enable the invasion of freshwater habitats and offer excellent systems for observing evolutionary adaptation in progress (Lee and Bell 1999; González-Wevar et al. 2015).

1.5.1. Limitations and further studies

Some otolith results may have been influenced by maternal effects or induced by local temporal variation in water chemistry. Further studies may indicate whether the higher Sr:Ca ratios in primordia observed in some species could be attributable to maternal effects or other causes. For example, although the mechanisms are not completely understood, physiological constraints in early ontogeny could increase the rate of Sr absorption into the calcium carbonate matrix of the otolith (de Pontual et al. 2003). Also, as the Baker river system is influenced by a large ice field (Campo de Hielo Norte), high amounts of glacier flour (suspended solids) can contribute to increased salinity levels in water that flows into the estuary (Vargas et al. 2011; Marín et al. 2013). These seasonal salinity changes may promote the uptake of Sr into the otolith matrix and confound the assumption of low Sr in freshwater environments (Zimmerman 2005). Therefore, even though Sr has been traditionally recognized as a very robust marker to discriminate between marine and freshwater environments, several recent studies have indicated that factors such as species-specific variation, environmentally-mediated physiological processes, individual variation and the interaction of different environmental factors can influence Sr uptake into the otolith matrix (Elsdon and Gillanders 2002a; Elsdon and Gillanders 2004; Gillanders 2005; Gillanders et al. 2015; Sturrock et al. 2015).

This study suggests that considerable variation in migratory life history may exist in Chilean fishes, but its inferential scope is restricted by the limited number of samples, which were collected for other research purposes (see Correa & Hendry, 2012; Correa et al., 2012; Alò et al., 2013) and by lack of water chemistry samples. The interpretations given for

diadromous and resident patterns are limited to the observed Sr:Ca shifts in the otolith profiles and should be considered carefully especially when referring to the extent of movement between different habitats. Species-specific reference values for Sr:Ca ratios and a more comprehensive sampling will be needed to quantify the extent of fish movements within Chilean continental waters in more detail. Ideally, a variety of different field techniques (natural markers such as stable isotopes, otoliths, statoliths for lampreys, or scales; as well as molecular markers, tagging, trapping and tracking) and laboratory methods (e.g. movement physiology, swimming performance, metabolism) (see Dingle, 2014) should be used to characterize daily and seasonal migration patterns. Incorporation of this knowledge could improve design and operation of fish passage structures to benefit native fishes (Laborde et al. 2016). However, because information on fish life history is lacking for native fishes in Chile and elsewhere in the temperate Southern Hemisphere, fish passage design is generally based solely on professional judgment (Wilkes et al. 2018).

1.5.2. Conservation issues

This study could help refine the conservation priorities for freshwater fishes in southern Chile. Given high endemism and the likelihood of dependence on diadromous behaviour, potential threats to fishes from fragmentation of river-to-estuary networks are correspondingly high. Hydroelectric power development causes loss of hydrological connectivity and alteration of the river flow regime, disproportionately affecting fishes with migratory life histories (Fullerton et al. 2010). Comparative otolith microchemistry results underscore the variation in life history strategies that should be accounted for when planning to manipulate water-flow for

hydroelectric developments. Diadromous species depend on the habitat diversity and complexity created by unobstructed watersheds and are locally extirpated when barriers preclude movement to essential habitat. Additionally, anthropogenic barriers and alterations to water flow (e.g., hydropeaking) may also negatively affect landlocked populations because such structures disrupt successful reproduction, recruitment and habitat quality (Alò and Turner 2005; Garcia et al. 2011). Current hydropower capacity in Chile (~6.000 megawatts of energy connected to the central grid) is expected to increase (~ 11.000 megawatts by the year 2020) building approximately 900 additional hydroelectric power plants due to legislative privileges given to hydroelectric investors such as i) water allocation rights favouring in-stream productive uses; ii) ease for hydropower investors to acquire riverside land; iii) specific tax easements and deferments for hydroelectric investors; and iv) taxes imposed for "ecological" in-stream uses (Prieto and Bauer 2012; Santana et al. 2014; Toledo 2014). Preliminary studies have identified most of the hydroelectric potential in the south-eastern sector of the country, in the sub-basins with high elevations and discharge (Santana et al. 2014). Development is slated in basins that harbour the majority of native fish species diversity.

Ongoing spread of exotic species threatens native species through negative interactions including predation, competition, behavioural inhibition and homogenization (Correa and Gross 2008; Penaluna et al. 2009; Correa et al. 2012; Correa and Hendry 2012b; Habit et al. 2012; Arismendi et al. 2014; Vargas et al. 2015). In particular, establishment of migration runs of *O. tshawytscha* and *O. kisutch* could trigger additional threats such as the shift of significant amounts of marine-derived nutrients to previously oligotrophic environments (Helfield and

Naiman 2001; Arismendi and Soto 2012) and increased competition for limited resources with the native diadromous species. Non-native salmon and trout are also likely to be negatively affected by future hydroelectric dams. Additional hydropower development will almost certainly impact a flourishing tourism industry supported by salmonid recreational fisheries (Arismendi and Nahuelhual 2007; Vigliano et al. 2007).

The evolutionary processes that allowed dispersal and colonization of Patagonian fishes are influenced by the region's unique geography, climate, and geological processes. To ensure conservation of native freshwater, diadromous, and commercially relevant sport fisheries, managers will have to carefully designate and protect critical habitats, and in many cases mitigate obstruction of river flows imposed by dams with appropriate fish passage structures (Wilkes et al. 2017). Long-term monitoring should also be a priority to understand the broad impacts of hydropower development on aquatic biodiversity.

1.6. ACKNOWLEDGEMENTS

2. CHAPTER TWO: Influence of environment and phylogeny on the global distribution of migratory fishes

Authors: Dominique Alò[1,2], Shaw Nozaki Lacy[3], Andrea Castillo[2], Pablo A. Marquet[1, 3, 4, 5]

[1]Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Santiago, Chile

[2]Laboratorio de Ecoinformática, Instituto de Conservación Biodiversidad y Territorio, Valdivia, Chile

[3]Centro de Cambio Global UC, Pontificia Universidad Católica de Chile, Santiago, Chile

[4] Instituto de Ecología y Biodiversidad (IEB), Santiago, Chile

[5] Laboratorio Internacional en Cambio Global (LINCGlobal, CSIC-UC)

Corresponding Author:

Dominique Alò

Email address: dominiquealo@gmail.com

Short Title: Global distribution of migratory fishes

2.1. ABSTRACT

Historical constraints and environmental conditions affect the emergence and evolution of life history traits that allow species to persist in ecological systems. One of these attributes, migratory strategies, has been the focus of several studies but as yet we lack a consensus on what constitute the main drivers of changes in these strategies. Fishes are particularly suitable for these kinds of studies, given their diversity of migratory strategies (e.g. diadromy, oceanodromy, potamodromy). For these groups, different hypotheses have been proposed in order to explain the spatial variation in the incidence of strategies: productivity, kinetic energy, environmental heterogeneity, and genetic predisposition. The objective of this work is to analyze fish migrations from a macroecological perspective to estimate the extent to which different environmental variables and historic biogeographic factors influence fish migratory life histories. Using data from public domain museum records, global repositories, and global measures of temperature, productivity, precipitation and heterogeneity, we spatially analyzed the distribution of migratory fish using 1799 species and compared it to 1602 non-migratory fishes. After analyzing the individual roles of productivity and temperature in shaping biodiversity, we conducted path analyses, including phylogenetic structure (PCPS). Results show that the different migratory strategies are not evenly distributed around the globe and that phylogeny is a relevant variable in shaping the current patterns. Productivity is positively related to species richness, except for anadromy and potamodromy, where we observed a unimodal curve, suggesting a dominant influence of competitive exclusion. Temperature significantly drives migratory species richness (except for anadromy), but in an indirect way. Overall, migratory fish richness can be explained by the interaction of multiple variables, such as productivity, temperature, environmental heterogeneity, and the role of phylogeny, but these variables interact differentially in each strategy. The role of environmental heterogeneity, measured as temperature seasonality and annual range is strongest for anadromous species, which helps explain their skewed distribution towards higher latitudes and why the kinetic-energy hypothesis fails in explaining their richness patterns.

Keywords: behavior, distribution, macroecology, fuzzy-weighting, heterogeneity, metabolic theory of ecology, PSRR, seasonal environments

2.2. INTRODUCTION

Movement is one of the underlining behavioral characteristics of life on Earth. All animals move at least at some stage within their lifespans, and one of the most fascinating types of movement, which has captivated the attention of both scientists and nonexperts, is migration. Animal migrations are recurrent within the animal kingdom and take place in many forms, habitats and taxa (Dingle 2014). Given this variability, it has been difficult to find common ecological and evolutionary features to explain migrations. Nevertheless, efforts to elucidate the reasons why animals undertake migrations have offered different perspectives that have been summarized by Dingle (2014) in a simplified model that accounts for the mutual relationship of migrants with their habitat, the effects of the habitat on the migrants through natural selection, which acts on the genome of the migrants to generate the migratory behavior. On the basis of Dingle's inclusive framework, a series of fundamental hypotheses may help understanding the relevance of different migratory strategies such as: i) *cost-benefit* approach, ii) habitat impact (through *productivity*, *energy*, *heterogeneity*), and iii) *genetic predisposition*. These hypotheses are part of a continuum of ecological and evolutionary explanations that together can contribute to a holistic model of migration (Dingle and Drake 2007; Pulido 2007; Dingle 2014).

The *cost-benefit* approach seeks to address why migration evolved and persisted, since the costs associated with migration are so high. If the benefit-to-cost ratio of moving exceeds

that for staying, migration should be favored by natural selection (Lack 1954; Dingle 2014), and fitness trade-offs in migrations occur if they are selectively advantageous over resident life histories (Gross 1987; Sword et al. 2005; Simpson et al. 2006; Bazazi et al. 2011). According to the *cost-benefit* hypothesis, abiotic factors and habitat characteristics should influence migratory behavior if they ultimately increase the fitness of migratory species. Therefore, as proposed by the *productivity hypothesis,* the direction of migration tends to be driven towards those habitats with larger resource provisioning (Gross, Coleman & McDowall, 1988) or triggered by resource scarcity (Buhl et al. 2006; Bazazi et al. 2011). Also, since the relationship between the energy available from the environment (*energy* as temperature) should directly affect species diversity with predictable patterns (Brown et al. 2004; Gillooly et al. 2005; Allen et al. 2006), migratory animals, with physiological adaptations and advantages conferred by their ability to displace, may show contrasting patterns of richness in relation to temperature. Migration confers both bioenergetic and evolutionary advantages to species adjusting to spatial and temporal habitat variation, and it is considered a metabolic necessity in seasonal environments (Seibert 1949; West 1960; Southwood 1962; McLaren 1963; Zimmerman 1965). Life at lower temperatures invariably involves coping with variations in resource availability, (i.e., *habitat heterogeneity*), and early research on the evolution of avian migrations suggested that migration might be a normal consequence of increased competition between and among species in seasonal environments (Cox 1968).

Although it has been suggested that migratory behavior is not dependent on phylogenetic inheritance, many of the morphological, physiological and behavioral traits

correlated with the triggering of migration require some *genetic predisposition* that confers a tendency for a "migratory syndrome" (Pulido 2011). Therefore, the evolutionary dynamics that might have shaped the current distribution and movement patterns among migratory species should be duly considered.

Migratory fishes represent an ideal group to test the ability of these hypotheses in holistically explaining the occurrence of different migratory strategies across the world, because migratory fishes present diverse strategies and relatively well-described distributions. Additionally, since the vast majority of fishes are ectotherms, their dependence on environmental changes should be predictable and dependent on energetics. In particular, fish species richness (log-transformed) appears to increase linearly with increases in temperature, according to the available *kinetic energy* of the environment, as proposed by the metabolic theory of ecology (MTE) (Gillooly et al. 2001; Allen et al. 2002; Brown et al. 2004). Additionally, some of the oldest fish taxa have been shown to be more likely to undertake migrations (McDowall 1997; Dodson et al. 2009; Bloom and Lovejoy 2014). Finally, from a biogeographic perspective, some areas seem more likely to be inhabited by migratory species than others (McDowall 1988).

Migration strategies in fishes have traditionally been described with reference to the aquatic environments in which they occur, with oceanodromy occurring entirely in oceans, potamodromy entirely in freshwater, and diadromy between marine and freshwater. Three different types of diadromy have been described, depending on the life history stages and zones at which each reproductive or feeding event occurs: anadromy involves birth in freshwater, migration to sea to grow and mature, and a return to freshwater to spawn.

Catadromy implicates birth in estuarine areas, migration to freshwater to grow, and return back to the ocean or estuarine areas to reproduce. Amphidromy also describes movements between freshwater and saltwater but these migrations are not driven by the purpose of feeding and/or reproduction (McDowall 1988; Dodson 1997).

The objective of this study is to analyze fish migrations from a macroecological perspective, testing to what extent global biodiversity patterns in migratory fishes are significantly related with environmental (productivity, temperature, and heterogeneity) and historical legacies, using the following scheme: First, we review global migratory fish diversity to reconsider and update prior work (McDowall 1988; Dodson 1997; Nelson 2006b) using global data on species occurrences and public-domain museum records. Second, we test for a direct relationship between biodiversity patterns of migratory species using productivity and temperature. Third, we test for the existence of interactions among explanatory variables explaining observed patterns by employing a path analysis approach, examining the joint relationship of several factors in shaping migratory species biodiversity, including productivity, temperature, environmental heterogeneity, and phylogenetic structure.

2.3. METHODS

Unless otherwise noted, all analyses were carried out using the R statistical package (R Core Team 2017).

2.3.1. Species taxonomic diversity and migratory life-history

Taxonomic information was obtained through Fishbase (Froese and Pauly 2016). This database compiles global fish records, free of synonyms, with a grand total 36,185 species (using R package *rfishbase* (Boettiger et al. 2012)), which amounts to the total recognized fish diversity, up to this date. From this database, we extracted the migratory life-history information, which included the categorical factors: "anadromous," "catadromous," "amphidromous," "oceanodromous," "potamodromous," and "non-migratory". All non-actinopterygii (other than ray-finned fishes) and records without an assigned category (NA) were discarded.

2.3.2. Species occurrence data

For each of the migratory and non-migratory species listed in Fishbase, we downloaded all available georeferenced records from the Global Biodiversity Information Facility (GBIF) using the *rgbif* library in R (Chamberlain 2017; R Core Team 2017). This was set to collect all unique records for each species that had coordinates and match these with their taxonomic and

life-history data (from Fishbase). The resulting database had a total of 1,799 migratory species and 1,602 non-migratory records with 1,919,586 and 824,318 occurrences, respectively, divided as shown in Table 4.

2.3.3. Data cleaning

Public records, while extremely useful, are still limited and biased by data type and availability. As more distributional data are uploaded onto public repositories, predictions in species distribution models will improve, but it remains necessary to filter the data in order to minimize the errors that frequently appear when using global repositories (Garcia-Rosello et al. 2015). We deleted 1) all records with NA values; 2) species with multiple records at a particular location; 3) records with identical geographic coordinates values for longitude and latitude (e.g., long = 0 ° and lat = 0 °); 4) records outside the habitat range, namely (a) oceanodromous species over continents, b) potamodromous over oceans, c) species in desert biomes without associated water bodies); and 5) exotic species.

To remove species that were potentially outside their habitat range, we used ArcGis Desktop, version 10.3 (ESRI 2012). Specifically, for point 4a and 4b the shapefile of coastal and shelf biogeographical areas from Spalding et al. (2007) was overlapped on the shapefiles of freshwater ecoregions (Abell et al. 2008b) and pelagic ecoregions (Spalding et al. 2012). All records of freshwater fishes in marine areas and marine fishes in continental areas were eliminated save for occurrences in coastal zones. Records associated with desert biomes, point 4c (Olson et al. 2001), were deleted if not associated with a water body, using a buffer zone of 50 km around the most important hydrological courses (Guan et al. 2012; Porto 2015). To

exclude locally exotic species (point 5), we used the "distribution" function in *rfishbase*, which provides records of the areas where the species are natives, according to FAO's fishing areas classification. This list was then employed to retain only native fishes using the fishing area classification shapefile (FAO 2014).

The cleaned data was assigned to equal-area cells (150km^2) and used to generate the species richness matrices, to map each migratory strategy in ArcGis Desktop version 10.3 (ESRI 2012) and to conduct path analyses.

2.3.4. *Environmental data*

Global layers of environmental data were only possible to obtain for productivity and temperature. The other variables differ between ocean and freshwater areas. WorldClim (Fick and Hijmans 2017) was used for freshwater-dwelling species (diadromous, potamodromous and freshwater-resident species) and BIO-Oracle (Assis et al. 2017) was used to test models in exclusively ocean-dwelling species (oceanodromous, and marine residents). Selected variables from WorldClim and BIO-Oracle were chosen based on how close the relationship to each other is (i.e. unidimensionality) in supporting the latent variables of the path analyses (Sanchez 2013).

Net Primary Productivity (NPP): To determine whether NPP is an important variable for any of the migratory strategies, we needed an estimate of both terrestrial and oceanic NPP. We used Moderate Resolution Imaging Spectroradiometer (MODIS) products of the Earth Observing System (EOS) from NASA, which can map global vegetation and derive the photosynthetic capacity of ecosystems. We used MOD17A3 for 2015, adjusted to g C/m^2/year

(Zhao et al. 2005) to reproduce estimates of global terrestrial NPP, based on the spectral radiance of the terrestrial surface. The MODIS-Aqua aboard the Aqua spacecraft records ocean color, and different algorithms can provide estimates of oceanic NPP through spectral radiance. We used the standard product from the Ocean Productivity site (Oregon State 2017), whose algorithm is based on a description of the Vertically Generalized Production Model (VGPM) (Behrenfeld and Falkowski 1997). We selected the 2015 estimates in mg $C/m^2/day$, which is a global product with a resolution of 1080×2160 cells (150km per cell), with NPP estimates provided for the world oceans. The units obtained for the ocean estimates of NPP were converted from mg $C/m^2/day$ to g $C/m^2/year$ to have a uniform NPP measure across land and ocean areas.

Temperature: Average land surface temperatures, representing climatic conditions from 1970 and 2000, were downloaded from WorldClim. We used average monthly temperature, with a spatial resolution of 30 arc-seconds (~1 km^2). Ocean surface temperatures were obtained from AquaMaps Environmental Dataset for the year 2011: Half-Degree Cells Authority File (HCAF) (Kaschner et al. 2008).

Each environmental data layer was processed in ArcGIS, georeferenced to WGS 1984 and reprojected to Cylindrical Equal Area constructing layers with annual average values. Numerical values of -9999 were transformed to "No Data," so as not to obtain incorrect average values.

Bioclimatic variables: Other environmental variables to be used for analyses in freshwater ecosystems were a subset of the WorldClim variables, which summarize terrestrial monthly temperature and precipitation information at a global scale. The bioclimatic variables available

represent annual trends, seasonality, and extreme or limiting environmental factors. For our analyses, we worked with 10 arc-minute spatial resolution (16 km at the equator).

Bio-ORACLE variables: To test models in oceanodromous species, we used a subset of the Bio-ORACLE environmental variables, providing geophysical, biotic, and climatic data for surface and benthic marine realms, obtained from the interpolation of remotely sensed data and *in situ* measured oceanographic data and surface measurements from the World Ocean Database 2009 (Tyberghein et al. 2012). We downloaded 16 average surface layers with a spatial resolution of 5 arc-minutes (approximately 9.2 km at the equator).

All the environment variables were divided into the same equal-area cells ($150km^2$) used for the fishes (see above), and used to generate the environmental matrices in ArcGis Desktop. Known or presumed indirect measures of productivity and heterogeneity (e.g. rainfall and chlorophyll or temperature seasonality and ice cover) were chosen as proxies to build the latent variables and to test different path models. However, selected variables were ultimately chosen based on their collinearity, predictive power, and capability in supporting the latent constructs (see Table 5 and Table S2).

2.3.5. *Phylogenetic Structure*

To include phylogenetic structure as an explanatory variable of migratory species richness, we relied on vectors that describe the phylogenetic gradient across a metacommunity assemblage known as principal coordinates of phylogenetic structure (PCPS), obtained using the fuzzy-weighting method outlined by Pillar & Duarte (2010). For each migratory and resident strategy, we calculated a phylogenetic matrix of pairwise dissimilarities using distances

averaged over the 100 full actinopterygians phylogenies published by Rabosky et al., 2018 using the R package *ape* (Paradis et al. 2004). After obtaining the phylogenetic structure of each assemblage, we performed a principal coordinate analysis and generated PCPS eigenvectors using the R package *PCPS* (van der Windt and Duarte 2014). Each of these orthogonal vectors describes different independent gradients in the dataset, the highest-value eigenvectors describe the differences at deeper nodes of the phylogeny, whereas the others describe shallower differences identifiable with more recent speciation events (Duarte et al. 2012; van der Windt and Duarte 2014). For each migratory strategy, we retained the main PCPSs that explained at least 60% of the variance in each assemblage, aiming at capturing the dissimilarities present at higher levels of the phylogeny (i.e. Order). Redundancy analysis (Borcard et al. 2009), carried out using the *vegan* package (Oksanen et al. 2017), assessed the relationship of phylogenetic dissimilarities obtained by the chosen PCPSs and weighed the differential importance of each of the environmental variable across the different clades.

2.3.6. Testing the productivity hypothesis

According to the *productivity* hypothesis, NPP should drive anadromous and catadromous fishes distributions, because oceanic NPP is higher than freshwater at temperate latitudes, anadromous species should be more common there, while freshwater productivity exceeds that of the ocean in tropical and lower latitude zones, where catadromous species prevail (Gross et al. 1988). To revisit this thirty-year-old hypothesis, we compared species richness values for each category to NPP (see above and Table 5). The shape of the relationship between productivity measures and species richness (PSRR) has been controversial (Mittelbach et al.

2001). Some authors have argued that a unimodal (hump-shaped) relationship is the "true" form of this relationship; others have shown that, positive relationships are more common, particularly among animals (Cusens et al. 2012). We calculated the shape of the PSRR using OLS regression (*glm* function in R) with the *stats* package and tested whether the quadratic component was significant ($P < 0.05$). If it was, we tested the significance of the hump (or pit) and its value using the *MOStest* function in the *vegan* package. The shape of the PSRR indicates whether and to what extent species richness in each migratory strategy increases with the productivity of the habitat measured with the global layer of NPP. Several outcomes are possible: i) a unimodal, hump-shaped curve describes a pattern where species richness increases as productivity increases up to a certain maximum and then decreases; ii) a u-shaped curve, where species richness drops as productivity increases, up to an inflection point, above which species richness changes very little with increasing productivity; iii) a monotonic positive relationship, where values of species richness increases along with productivity; iv) monotonic negative, where species richness decreases linearly as productivity increases, and v) neutral (Cusens et al. 2012; Shipley 2016; Chen et al. 2018).

2.3.7. *Testing the kinetic energy hypothesis*

According to Allen et al. (2002), the slope for the relation between diversity and temperature should be linear along latitudinal gradients, based on the role of temperature on metabolic rate as shown by the metabolic theory of ecology (Brown et al. 2004), such that the natural log of species richness should relate linearly with $1000/T_{env}$, and the slope should approximate $-E/1000\,k \approx -9.0\,K$ (absolute temperature). To test whether migratory and non-migratory

species follow the same general predicted trends, we used the log-transformed number of species at 5-degree latitudinal bands (36 in total) for each migration strategy and plotted them against 1000/average of the absolute temperature. The 95% confidence intervals were calculated for the slope of each linear relationship obtained.

2.3.8. *Path analyses*

We used path analysis to define the relative importance of *a priori* hypotheses in shaping migratory species diversity. In particular, trying to assess several hypotheses (*productivity*, *kinetic energy*, *heterogeneity*, *genetic predisposition*), we constructed a model that represents the interactions and relationships of several variables simultaneously influencing species richness and separately tested each dataset of migratory/resident strategies. We hypothesized that direct and indirect productivity measures (i.e. NPP and precipitation), temperature, environmental heterogeneity, and phylogenetic structure interact at different levels to influence species richness in migratory species. With the construction of this model, we argue that single factors cannot be invoked as being uniquely responsible causal mechanisms of migratory species diversity, but that it is the interplay of different variables that shapes migratory species biodiversity.

We started the path analysis by defining the hypothesized causal relationships between the factors that affect migratory species biodiversity and represented these associations with a causal diagram (Shipley 2016). A partial least-squares path modeling (pls-PM) approach was employed to test our model to accommodate non-metric data. Pls-PM is a statistical, exploratory method for studying complex multivariate relationships among observed

(manifest) and latent variables. Latent variable constructs cannot be measured directly, but they represent entities that influence the dependent variable through a suite of measurable independent variables (Sanchez 2013). For example, "heterogeneity" is an abstract, non-measurable term that has been operationalized in different ways in various studies. In this study, the latent variable *Heterogeneity* describes the state of a changing environment, and is represented by specific manifest variables that reflect such changes. Therefore, "seasonality" (*BIO4*), "temperature annual range" (*BIO7*), "mean diurnal range" (*BIO2*), and "isothermality" (*BIO3*) were WorldClim variables selected to represent *Heterogeneity* in diadromous, potamodromous, and freshwater-resident species. Since the same independent variables were unavailable for oceanodromous and ocean-resident species, *Heterogeneity* for ocean species was represented by "ice cover" (*icec*), "ice thickness" (*icet*), "cloud cover" (*clo*) and "current velocity" (*vel*).

All the manifest variables influencing (reflective mode) a latent construct need to demonstrate to be reliable at measuring the same concept. Therefore, among the variables chosen to build a specific latent variable, only those highly correlated and homogenous would be considered useful to be used in the path model. Only variables with Cronbach's alpha > 0.7, Dillon-Goldstein's rho > 0.7 and first eigenvalue of the indicators' correlation matrices > 1.0 were included in the models (Vinzi et al. 2011; Sanchez 2013). *Richness* (*sr*) was included in the model as a direct construct (no manifest variables). The PCPSs were used as explanatory variables representing historical structure of the distribution of the migratory and resident groups. All latent variables included in the model are listed in Table 5, along with their respective manifest variables. The path coefficient estimates of the hypothesized model were

carried out using the *plspm* package (Sanchez 2013). The relevance of each assessed relationship was measured using bootstrap validation (999 samples). Variable transformation prior to analysis were conducted as follows: i) to reflect in the path analysis the same direct relationship between species richness and temperature (all WorldClim variables related with temperature went through the same transformation) as $temp = -1000 \div (temp + 273.15)$; ii) natural logarithm +1 for *sr, npp, BIO12, BIO14, BIO17, BIO18, BIO19.*

2.4. RESULTS

2.4.1.   Frequency of migratory life-histories in fishes

The total number of fish species resulting from the search and download of the Fishbase data repository were 33,096. Among these, 2.2% of total world fish biodiversity were oceanodromous, 1.7% potamodromous, 1.4% amphidromous, 0.5% anadromous, and 0.2% catadromous. All migratory fishes represent 6.9% of global fish diversity, while diadromous fishes represent 2.4% (Table 4).

2.4.2.   Migratory fish diversity

The different strategies of migratory fishes are not evenly distributed around the globe. Maps of species richness for each migratory strategy (Fig. 7) suggest that anadromous species do not increase towards the equator, as most species. This observation is reinforced by examining species richness counts along latitudinal ranges (Fig. 8), with the highest anadromous richness counts occurring between 40 °N and 50 °N. In contrast, maximum catadromous species richness is found between 10 °S and 30 °S, although the shift in maximum species richness from 0° latitude is not as pronounced as among anadromous species. In general, the highest diversity for both amphidromous and potamodromous species is between 10 °N and 20 °N. Oceanodromous species, in contrast, show uniform levels of species richness between 30 °S

and 30 °N, with higher numbers in the Northern Hemisphere. A list of the ecoregions (Spalding et al. 2007; Abell et al. 2008a) with the highest biodiversity for each migratory strategy is presented in Table 4.

2.4.3. Productivity hypothesis

Results from the PSRR show that the relationship between species richness and productivity in fishes is either unimodal with a hump-shaped curve (anadromous and potamodromous species) or monotonic positive (the rest of the strategies analyzed, see Table 6). The quadratic component was negative in all strategies (not significant in amphidromous and ocean resident fishes). Groups with a significant quadratic component were subjected to a MOStest, which supported a hump-shaped distribution only for anadromous and potamodromous fishes. This means increasing productivity generates higher species diversity up to a certain point (hump 639.0 $gC/m^2/year$ and 906.0 $gC/m^2/year$, for anadromous and potamodromous species respectively). The rest of the categories showed evidence of a positive linear (accelerating positive) relationship, meaning increasing productivity leads to continuous increases in species richness (Table 7).

2.4.4. Kinetic-energy hypothesis

The linear relationship between the log of species richness and 1000/average of the absolute temperature shows that, as predicted by Allen, Brown, & Gillooly (2002), the kinetic energy of the environment significantly influences biodiversity of all migratory and non-migratory

species, except for anadromous fishes. In fact, residuals for anadromous species show more variation suggesting that other variables are important in affecting species richness of fish adopting these strategies (Fig. 9, Table 7). Additionally, one of our main objectives was to find out whether the energy/biodiversity patterns between migratory fishes and residents vary in response to the temperature of the environment. A comparison of regression models with migratory/resident strategies as categorical effects indicated that the slope and intercept of all migratory strategies significantly departed from the grand mean (ANOVA, p-values < 0.001), whereas non-migratory fishes did not differ from the grand mean (p-values > 0.1).

2.4.5. Path analyses

According to the hypothesized causal diagram of Fig. 10, migratory fish biodiversity is simultaneously influenced by several factors. The proposed model was tested for all relationships listed, and the coefficients obtained in the path analyses indicate the strength and direction (positive or negative effects) of a relationship between two variables. When the bootstrap confidence intervals overlap zero, the effects of the relationship between the two variables are not considered significant. Only the latent constructs shown in bold in Table 5 were used to test the model for each strategy. Additionally, relationships with bootstrap confidence intervals overlapping zero were removed from the models (see Fig. 10 and the path diagrams in Figure S1).

Each path analysis is supported by a Goodness of Fit (GoF) value that represents a pseudo-R^2, where values of 0 indicate no relationship and values of 1 indicate that the variability of species richness is fully explained by the proposed variables (Henseler and

Sarstedt 2013). Results from path analyses (Fig. 11 and Fig. S1) show that net effects of *Productivity* are positively associated with species richness in all migratory strategies and strongest (path coefficients ~ 0.2) in anadromy, catadromy, oceanodromy, and non-migratory ocean and freshwater species. Weaker associations are observed for potamodromy, and amphidromy. *Temperature* has a net positive relationship with species richness in all migratory strategies, however a direct relationship is seen only in most non-diadromous fishes (i.e., oceanodromous, potamodromous, and ocean residents). Interestingly, species richness across all diadromous species is positively related to *Temperature* only via indirect relationships with other variables (Supplemental Figures S1) (e.g. in catadromous species, *Temperature* → *Precipitation* / *Productivity* → *Richness*). *Heterogeneity* showed the highest positive effect in anadromy (path coefficient: 0.19). Catadromous species richness is also affected by significant positive direct and indirect relationships with *Heterogeneity* (path coefficients: 0.16); whereas amphidromous species richness is affected by positive direct and negative indirect effects, leading to a net weaker interaction (path coefficient: 0.08). Oceanodromous species richness shows a negative relationship with *Heterogeneity*, supported by both direct and indirect path effects. The effects of *Precipitation* on species richness were evaluated exclusively for freshwater-dwelling species and showed a positive relationship for most examined migratory strategies (except potamodromous), driven by both direct and indirect effects.

In our explanatory model, PCPSs were hypothesized to be directly related to species richness (Fig. 10). Our results show that these vectors can relate either negatively or positively to species richness. For example, PCPS.1 is positively related to species richness in anadromy,

but its relationship is negative in amphidromy. This suggests that this vector, which is a phylogenetic filter based on evolutionary distances between species, is positively associated with species richness at locations occupied by anadromous species, and negative for those occupied by amphidromous fishes. The observed relationship between PCPS.1 and anadromy and amphidromy is further explained by looking at the RDA ordination (Fig. 12) of species richness constrained with PCPS filters and selected environmental variables, which shows how different clades (Orders) relate to phylogenetic vectors. For example, Fig. 12A shows how salmonids are negatively related to PCPS.1 and mostly correlated with environmental heterogeneity but other clades, such as the Clupeiformes are strongly associated with the PCPS.1 vector.

Overall, all factors of causality included in the exploratory structural model affect the biodiversity of migratory fishes. These interactions can be direct or indirect, negative or positive, depending on the different migratory or resident strategies (Fig. 11).

2.5. DISCUSSION

Several hypotheses thought to influence species richness in migratory species were tested to assess the major factors that drive the migratory fish richness. Specifically, we tested the *productivity hypothesis* proposed by Gross, Coleman & McDowall (1988) and the *kinetic-energy of the environment* hypothesis, proposed by Allen, Brown & Gillooly (2002) to see whether each hypothesis could individually explain biodiversity patterns of migratory species. Since results were ambiguous (especially for anadromy), we integrated multivariate analyses into a path modeling approach, in order to test multiple hypotheses within a single framework and discern hidden relationships among variables. We tested different hypotheses through a series of exploratory path analyses, evaluating the contribution of additional variables thought to influence migratory-species richness, such as precipitation, heterogeneity, and phylogenetic structure. The most important observations stemming from this work were that: i) biodiversity is strongly dependent on the productivity of the environment (PSRR) in migratory and resident fishes alike, although in anadromous and potamodromous species this relationship shows evidence of unimodality for anadromy and potamodromy, where species richness increased to a certain threshold and then started decreasing; ii) temperature is an important variable in driving biodiversity, but its influence is indirect in diadromy and even less relevant in anadromy, iii) the role of environmental heterogeneity is the strongest for anadromy, which helps explain their skewed distribution pattern towards higher latitudes and low fit within the

kinetic-energy hypothesis; iv) migratory fish richness can be explained by the interaction of multiple variables, such as productivity, precipitation, temperature, environmental heterogeneity, and phylogenetic structure, and these variables interact differentially in each strategy.

2.5.1. *Overall geographic patterns in migration strategies*

Probably because of the high costs involved in undertaking migrations (Gross 1987), only a minority of all fishes worldwide exhibit migratory strategies, and the distribution of migratory fish species richness is not globally uniform. While some of this non-uniformity might relate to bias in sampling methods, the majority is more likely to be intrinsically related to evolution and biogeography. For example, anadromous species follow an inverse pattern of species richness to the majority of species on Earth, with peaks in richness observed in temperate zones (e.g. the Baltic and North Sea, Northern Atlantic, Celtic Seas, and the Laurentian Great Lakes). Catadromous species, in comparison, occur mostly in very different areas, favoring ecoregions with higher temperatures (e.g. the Zambezian Lowveld of Mozambique, the eastern and northern coasts of Australia, and the coasts of East Asia). Amphidromy appears to have a strong geographic overlap with catadromy, although it is more constrained to tropical waters. Potamodromy, in contrast, is concentrated in West Africa, South and Southeast Asia, the Amazon-Orinoco, and Western Europe. Oceanodromy tends to be found in areas with broad continental shelves (e.g. the Gulf of Mexico) and/or strong warm oceanic currents (e.g. the Gulf Stream, the Alguhas Current, the East Australia Current, and the Kuroshiro Current).

The latitudinal richness pattern has traditionally shown how most species follow a latitudinal gradient of increasing species diversity from the poles to the equator (Rohde 1992; Brown and Lomolino 1998; Gaston 2000; but see Valdovinos et al. 2003). This study shows anadromous species along a very different gradient, with peaks in species richness between 40 and 50 degrees north latitude, and no native species richness patterns in the tropics or Southern Hemisphere. This particular pattern speaks strongly of the historical legacy of this migration strategy, being constrained to species that are from families characterized by cold-stenothermy (McDowall 2008). While the evolution of anadromy can be associated with high NPP in high-latitude coastal waters, this trend is countered by the presence (albeit lower) of anadromous fishes at lower latitudes, and the lack of anadromy in the high latitude waters of the Southern Hemisphere, save for a handful of species in Australia and New Zealand (Gross et al. 1988). However, most of the actinopterygian anadromous species in the Southern Hemisphere are better described as semi-anadromous, whose non-marine life stages are in estuarine areas and the lowest reaches of rivers (Miles 2007), unlike the life history patterns of Northern Hemisphere anadromous species, many of whom can be found throughout river systems in different periods of their life cycles.

Other migratory strategies do appear to broadly follow the species-latitude pattern, with maximum species richness found at low latitudes in the Southern Hemisphere for catadromy, and low latitudes in the Northern Hemisphere for both amphidromy and potamodromy. A large part of the patterns seen for amphidromous and potamodromous species richness appears to be associated with the amount of river area coverage, which is greatest near the equator and at high northern latitudes. In fact, south of 20 °S, non-tropical

Southern Hemisphere rivers are narrower and shorter than Northern Hemisphere rivers at that same latitude (Allen and Pavelsky 2018). This significantly limits the amount of comparable habitat available at complementary latitudes between hemispheres. Furthermore, the relatively higher levels of historic isolation between Southern Hemisphere landmasses, including between Australia and Southeast Asia (Unmack 2001), means that movement between landmasses is far less apparent, although there are exceptions (McDowall 2002c). These physical distinctions between hemispheres could help explain the lower levels of diadromy and potamodromy in the extra-tropical Southern Hemisphere.

The relatively more-constrained latitudinal distribution of potamodromy could be explained by the impacts of historical events, especially glaciation (*sensu* Svenning et al. 2015), and this appears to be the case at latitudes higher than 45° North and South, where potamodromous species richness abruptly decreases from the strongly unimodal distribution found most elsewhere in its latitudinal range (Figure 2). In both hemispheres, the river basins at these high latitudes were heavily affected by glaciation during the Last Glacial Maximum, meaning that freshwater-dependent species, being unable to take advantage of marine dispersal, would have been extirpated. Exceptions would be where species could take advantage of greater river connectivity due to exposed continental shelves (Ruzzante et al. 2008; Dias et al. 2014), where species lived in north-south orientated river basins that were sufficiently large so as to have non-glaciated extents, or where species were able to recolonize previously glaciated basins during glacial retreat (Oberdorff et al. 1997; Griffiths 2015).

2.5.2. Fish migratory strategies are influenced by phylogeny and spatial legacies

Our study indicates a strong influence of phylogeny on the current distribution of migratory species, showing that fish belonging to a particular migratory strategy tend to occur in delimited regions and partition mostly according to their clade structure (i.e. Order). This suggests that each migratory strategy not only falls within a specific set of adaptations and behavioral characteristics, but also that each strategy is linked to a specific time and place of origin (Lévêque et al. 2008). That is, speciation from a single ancestor with specific characteristics which gave rise to a series of descendants, with all (or nearly all) following the same specific behavioral migratory strategy (Dodson et al. 2009). The phylogenetic effects are more apparent in diadromous species, as all require specific physiological and ontogenetic adaptations to cope with a changing environment, with only occasional instances of species losing their migratory potential (e.g., *Galaxias paucispondylus*) (Dunn and O'Brian 2007). Oceanodromous and potamodromous species do not depend on physiological mechanisms to migrate through osmotic barriers, and thus different evolutionary and ecological drivers may influence their dependence on phylogenetic structure and their diversity is most likely shaped by the physiological adaptations needed to cope with stressful environments, competition, and predation.

2.5.3. Productivity hypothesis

Productivity drives species richness in migratory and resident species, although for anadromy and potamodromy, this relationship holds only to a certain point, and then species richness decreases as productivity increases. This unimodal relationship suggests that, when

productivity exceeds the optimal values, only some species benefit from increasing environmental resources. Biotic interactions, such as predation, may play a more important role in anadromy and potamodromy, compared to resident and the other migratory strategies, which showed monotonic positive PSRR. These data partially support Gross' *productivity hypothesis,* as migratory species tend to increase in areas of higher productivity (with the exception of anadromous and potamodromous species). While we did not explicitly test whether ocean productivity exceed freshwater, as Gross' *productivity hypothesis* suggested, although anadromy does show a higher incidence in the Northern Hemisphere, where the ocean is more productive, freshwater areas support more species than nearby oceans at the same latitudes, and the Southern Hemisphere fails to show any similar trend. Additionally, our analysis has shown that productivity provides a significant causal relationship for species. Anadromy and potamodromy could be seen as strategies evolved to avoid competition in unproductive environments during certain stages of the lifecycle. Further research on evolutionary transitions between marine and freshwater habitats may help explain the observed patterns (see Dodson, Laroche & Lecomte, 2009; Bloom, 2013; Bloom & Lovejoy, 2017).

2.5.4. Kinetic energy hypothesis/Metabolic theory

While most migratory species show a positive relationship with temperature, with species richness increasing linearly with increasing temperatures, anadromy does not show this trend. Additionally, all migratory species show a slope in the linear relationship that departs from MTE predictions of -9K, suggesting that the temperature-species richness relationship in

migratory species is different, showing, for example, that many oceanodromous species are able to dwell at lower temperatures compared to other analyzed strategies (Figure 9). Also, path analysis suggests that the temperature-species richness relationship becomes less relevant when other variables are considered, meaning that temperature cannot be the sole predictor of species presence. Water currents (driven by winds and global atmospheric circulation) and temperature seasonality, coupled with thermoregulation, heterogeneity in nutrient availability, and specific adaptations to cope with environmental harshness (therefore phylogeny), could be some other possibilities driving species richness. The strong departure from the *kinetic-energy* hypothesis in some migratory species warrants further research into the role of metabolism regulating biological activities for these fishes. As mentioned above, anadromous fishes are dominated by cold-stenothermal species, (i.e., salmonids), but even when these are excluded, there is still a marked preference for cold waters (McDowall 2008). Among oceanodromous fishes, regional (partial) endothermy is known to occur in Lamnid sharks and tunas, with all Lambridae and Scombridae being oceanodromous. Adult Atlantic bluefin tuna (*Thunnus thynnus*) can maintain relatively stable body temperatures (~25 °C) even when traversing waters as cold as 3 °C. In the salmon shark, *Lamna ditropis*, the enhanced expression of some proteins helps mitigate the effects of low water temperatures. However, these forms of endothermy arose independently and are driven by different physiological processes (Dickson and Graham 2004). Recently, the discovery of a completely warm-blooded fish, the oceanodromous *Lampris guttatus*, has shed more light on the key-evolutionary adaptations needed to cope with cold waters in this evolutionary line (Porch 2005; Wegner et al. 2015). Further research in migratory fishes, looking for adaptations at the interface with a warm-

blooded metabolism, may help with understanding the extent to which endothermy has played a role in the evolution and maintenance of certain lineages of fishes.

2.5.5. *Limitations and future studies*

These data were obtained from public, global repositories, and both spatial, temporal and categorization bias can affect results. In particular, there was no geospatial data available for northern Eurasia (i.e. Russian Federation, where native migratory species are known to exist, such as the endangered potamodromous *Hucho taimen*), and the distribution of fishes from China was highly imprecise, as nearly all fish data were concentrated in the Gobi Desert, and were therefore removed during data cleaning.

Similarly, the assessment of five categories of migratory behavior across 1913 species, 221 families, and 37 orders inherently means that there are "degrees" within the spectra of migratory behaviors that have not been sufficiently described. For example, *Lovettia sealii* (Tasmanian whitebait) and *Oncorhynchus tshawytscha* (Chinook salmon) are both classified as anadromous, but the "degree" of anadromy between these two species is extreme. Also, *Thunnus thynnus* (Atlantic bluefin tuna) and *Clupea harengus* (Atlantic herring) are both oceanodromous, but have vastly different migratory ranges. Some of these differences can be associated with body size, with larger fish species typically having larger movement capabilities (Woolnough et al. 2009; Radinger and Wolter 2014). However, such degrees of diadromy likely have a strong evolutionary component, given the importance of genetics and epigenetics in governing the physiological and behavioral changes associated with catadromy and anadromy (Hecht et al. 2012; Baerwald et al. 2016).

Some migratory fishes are given multiple, different classifications, and this seems especially true for diadromous, potamodromous, and euryhaline fishes. Often fish demonstrate capacity for multiple types of migratory behaviors, and, depending on their habitat, they have been classified according to multiple strategies. For example, *Galaxias maculatus,* (Puye in Chile or Inanga in New Zealand) has been shown to be a facultative migrant, and has been classified as amphidromous, catadromous, and – for landlocked populations – either exclusively freshwater-resident or potamodromous (Górski et al. 2015; Ruiz-Jarabo et al. 2016; Alò et al. 2019). Similarly, many salmonids have migratory and non-migratory forms, with *Oncorhynchus mykiss* being a classic example (Hecht et al. 2012; Baerwald et al. 2016), but are defined as anadromous in the database, regardless of the presence of any connection to a marine setting.

Finally, evolutionary heritage is only assessed in the context of modern-day continental positions and climates. Incorporating paleogeography (Albert and Reis 2011) could help uncover additional pieces of evidence that could help elucidate how current-day species distributions and intervening speciation and extinction rates have led to current distributions of species richness.

2.5.6. *Concluding remarks*

Fish migrations are driven by multiple ecological and evolutionary processes. We could not isolate single factors as uniquely responsible for migratory fish biodiversity. In this paper, we examined and tested whether specific environmental characteristics could be pinpointed as responsible for explaining species richness in several migratory strategies. We found that

productivity, temperature, and heterogeneity interact to affect the biodiversity of migratory species. We also highlighted that the role of history has a strong impact in shaping the global distribution of these species. There are different patterns for each migratory strategy, and multiple environmental variables can relate to migratory strategies in different ways. For example, the role of seasonality (*heterogeneity*) is much stronger in driving species richness in anadromy than the other strategies, while the role of *productivity* seems important in driving diversity of all species.

Increasing our understanding of how these different migratory strategies interact with spatial and environmental variables as well as the legacies of their evolutionary histories may help predict their responses to climate change and human disturbances. Migrating fishes represent only 6.9% of the total fish diversity, and some of them are severely challenged from a conservation perspective. Therefore, the consequences of ongoing global climate change, land-use change, invasive species, river alterations, and water obstructions (Arthington et al. 2016) can be expected to be particularly troubling for many migratory species, especially for diadromous species. Worldwide, many migratory fish species are also highly important for fisheries, such as diadromous salmonids, clupeids, sturgeons, etc. or marine fishes, such as those in the Scorpanidae family, which have a cosmopolitan distribution and high dispersal capabilities thought to be influenced by their migratory patterns (Gonzalez et al. 2008), but are also a globally important human food source. Therefore, some of the relevant characteristics that make a fish species commercially important may also be relevant from the standpoint of migration, and warranting further research.

This work sought to test different existing hypotheses (*productivity*, *kinetic energy*, *environmental heterogeneity*, and *genetic predisposition*) in support of developing a holistic model of migration (Dingle and Drake 2007; Pulido 2007; Dingle 2014). Our results insert well into a global framework of migration, showing how current biodiversity patterns discerned among different migratory strategies can be explained by the joint effect of multiple environmental and productivity variables, and, additionally, how biodiversity is influenced by the role of historical factors constrained by phylogeny.

2.6. ACKNOWLEDGEMENTS

3. **CHAPTER 3:** Speciation rates, latitude and migratory life-history in fishes

Authors: Dominique Alò[1, 2], Leonel Herrera-Alsina[3], Pablo A. Marquet[1, 4, 5]

[1] Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Santiago, Chile

[2] Laboratorio de Ecoinformática Instituto de Conservación Biodiversidad y Territorio, Universidad Austral de Chile, Valdivia, Chile

[3] Groningen Institute for Evolutionary Life Sciences, University of Groningen, PO Box 11103, Groningen 9700 CC, The Netherlands

[4] Instituto de Ecología y Biodiversidad (IEB), Santiago, Chile

[5] Laboratorio Internacional en Cambio Global (LINCGlobal, CSIC-UC)

Correspondence: Dominique Alò, dominiquealo@gmail.com, Tel: +56 (9) 53348887, ORCID 0000-0003-0579-4156

3.1. ABSTRACT

Diversification rates are expected to follow patterns dictated by the latitudinal gradient of species richness, with higher diversification rates at lower latitudes. However, species dispersal capabilities should also influence the dynamic of the diversification rates. Migrations allow species to colonize new habitats, avoid extinction, and increase gene flow. Migratory fishes have a tendency to group within just a handful of families and fishes within older taxa are more likely to undertake migrations. This phylogenetic propensity for selected taxa to migrate suggests that most migrating fishes may have had a different diversification history compared to resident species. This study aims to detect whether the diversification dynamics of migratory fishes are different to those of resident fishes. We assessed phylogenetic distinctiveness using a comparative approach using the most recent actinopterygian fish time-calibrated phylogeny and tested for state-dependent evolution of traits dependent on movement capabilities and latitude. We found that migrants are different from residents, where anadromous and migrating fishes in general display faster speciation rates. We also found evidence that speciation rates are higher at lower latitudes. There is evidence that an additional, concealed trait is driving speciation rates. Evidence shows that in the Southern Hemisphere faster speciation rates occur at lower latitudes in continental fishes and at higher latitudes in marine fishes, whereas in the Northern Hemisphere anadromous fish prevail at high latitudes and the rest of the fishes are mostly concentrated at lower latitudes. Several migratory species represent evolutionary legacies of the past. Specific management and conservation measures should be taken into account, especially considering that climate change and temperature increases will severely affect the heterogeneous, temperate environments occupied by many migratory fishes.

Keywords: diadromy, diversification rates, oceanodromy, potamodromy

3.2. INTRODUCTION

It has long been observed that species diversity across the globe follows a latitudinal gradient pattern (LDG), with higher diversity observed at the tropics and lower diversity at higher latitudes (Hillebrand 2004). Several different hypotheses have been offered to explain the reasons of this biogeographical phenomenon. In particular, the diversification rate hypothesis (DRH) posits that given the higher temperatures of low latitudes, physiological and genetic mechanisms occur at a faster rate, leading to higher mutation rates and therefore higher speciation and diversity. Also, the tropical conservatism hypothesis (THC) proposes that given the earlier origins of tropical environments, extra-tropical species are generally evolutionary younger and nested within tropical clades (Mittelbach et al. 2007; Economo et al. 2019).

We argue that dispersal capabilities should affect the outcome and support of the two hypotheses presented above. In fact, there should be differences in species distribution, speciation rates, and evolutionary times given different types of life-history and different ability to disperse. Migration is one particular type of dispersal strategy, and can be seen as an adaptive response to seasonal environments. All animals should display the capacity to migrate given the right environmental and biological pressures (Pulido 2007), however, some lineages show a higher propensity of expressing or maintaining the migratory trait, (e.g. in fish: lamnid sharks, lampreys and clupeiform) (McDowall 1997; Dodson et al. 2009; Bloom and Lovejoy 2014). This is because of the complexity of the migratory conduct, which entails

the synergy in the expression of different characteristics of anatomy, behaviour and physiology that may facilitate migration in some groups and hinder it in others.

Fish offer excellent opportunities to study LDG and diversification patterns given different scenarios and hypotheses as they are widely distributed across the globe, they have relatively defined life-history strategies and a well-studied phylogeny, partially supported by genetic data. In fact, different migratory categorizations exist to classify fish. If not exclusively resident in one habitat (marine, freshwater or brackish), fish are classified as either oceanodromous or potamodromous when their range shifts occur within ocean and freshwater, respectively. On the other hand, diadromy is a term that indicates migratory shifts across freshwater and saltwater, and includes anadromy, catadromy and amphidromy. Anadromy and catadromy are subclassifications of diadromy that refer to the direction of the migratory movement and are triggered by either reproduction or feeding. Amphidromous migrations are not defined from the purpose of reproduction, and can be defined by fish travelling in both directions (Myers 1949; McDowall 1992; Northcote 1997).

A recent study that looked at the relationship between species diversification rates and LDG in fishes (Rabosky et al. 2018) found an inverse gradient of diversification rates in marine fishes, with species at very high latitudes (Artic and Antarctic) displaying higher rates than tropical species. In this paper, we expand on Rabosky et al. (2018) work, asking whether the inclusion of additional life-history strategies (freshwater, brackish and migratory) would lead to the same conclusions. Specifically, we argue that we should expect lower speciation rates in migratory fishes as they do not speciate as much as sedentary species because they are either equipped with specific adaptations that allow them to move instead of perishing or they

are generally less able to solve problems of ecological isolation by morphological differentiation (Cox 1968). Migration strategies are selected and maintained by natural selection through differential mortality and the probability of extinction decreases if a species migrates (von Haartman 1968; Roff 1990). Migration also increases gene flow, thereby decreasing the likelihood of speciation events (McDowall 2001).

In order to test the hypotheses based on the above observations, we deconstruct the role of specific migratory and resident strategies in contributing to different scenarios. In particular, i) we question whether Rabosky et al. (2018) findings can be applied to the entire fish phylogeny, including fish from different habitats and life-history strategies; ii) we ask whether the majority of species with higher diversification rates at high latitudes are mostly resident species, possibly going through major adaptive radiations given the relative habitat youth of current temperate habitats; iii) we test whether taxa with predisposition to migration could have had a different diversification history (due to ecological and/or geological factors) and whether we can detect a distinctive evolutionary signal when comparing migratory species to resident species.

If migratory species were subjected to different evolutionary constraints or pathways compared to their resident counterparts and at different latitudes, a signal should be detectable by measuring phylogenetic distinctiveness (Redding and Mooers 2006; Vellend et al. 2010; Friedman et al. 2017; Economo et al. 2019). We used a comparative approach using phylogenetic data from the most recent Actinopterygian backbone phylogeny (Rabosky et al. 2018) and included geographic information.

3.3. METHODS

Unless otherwise noted, all analyses were carried out using the R statistical package (R Core Team 2017).

3.3.1. *Species taxonomic diversity and migratory life-history*

Taxonomic information was obtained through Fishbase (Froese and Pauly 2016). This database compiles global fish records, free of synonyms, with a grand total 36,185 species (using R package *rfishbase* (Boettiger et al. 2012)), which amounts to the total recognized fish diversity, up to this date. From this database, we extracted the migratory life-history information, which included one column (AnaCat) with the categorical factors "anadromous," "catadromous," "amphidromous," "oceanodromous," "potamodromous," "non-migratory," and "NA" (no category assigned) and three columns of specific habitat information in binary state, which included "Saltwater", "Fresh" and "Brack" species. All non-ray-finned fish (non-actinopterygii) records were discarded. Since the "non-migratory" category is somewhat arbitrary, as it leaves out the rest of most fishes, we introduced some changes to the Fishbase categorization. In general, it has been recognized by several authors that very few fishes among the ~32,000 recognized species display migratory behavior. This is, of course, arguable, as probably many more fishes, among those officially recognized as within some migratory category, display some form of displacement throughout their lifetime. For the sake

of this study, we are making the assumption that most conspicuously migratory fishes have been categorized and recognized, and these, given the high cost associated with migratory behavior are very few, as recognized in the literature (McDowall 1987; Nelson 2006a), who have suggested that only 2% of migratory fishes are diadromous (osmoregulatory migrants, that is anadromous, catadromous and amphidromous). Therefore, group categorizations were carried out as follow: assigned "Marine" to all fish with "NA" or "non-migratory" in the AnaCat column and "1" in the "Saltwater" column, assuming these are all marine fishes; assigned "Freshwater" to all fish with "NA" or "non-migratory" in the AnaCat column and "1" in the "Fresh" column, assuming these are all freshwater fishes; assigned "Brackish" to all fish with "NA" or "non-migratory" in the AnaCat column and "1" in the "Brack" column, assuming these are all brackish water fishes. Some non-migratory fishes were listed as present in more than one habitat (Fresh and Brack, or Brack and Saltwater, or Fresh/Brack/Saltwater), as they could not be assigned to a single habitat category, they were marked as "NA". All those fishes that didn't have any AnaCat category assigned ("NA") and more than one habitat listed were assigned to the "brackish" category. In this way, we removed the "non-migratory" category but added three categories of marine/freshwater/brackish fishes, which could be grouped into a unique "resident" category.

3.3.2. *Phylogenetic tree*

Phylogenetic trees can be used to track the changes in the number of species through time and allow the possibility of testing a variety of hypotheses and model fitting. The most up-to-date time-scaled classification of the Tree of Life of fishes (Rabosky et al. 2018) was used. This

tree includes a total of 11,638 species generated by a 27-gene multilocus alignment and a maximum likelihood topology for ray-finned fishes. Supplementary information of the aforementioned phylogenetic tree provided estimates of time-varying speciation rate regimes (λ_{BAMM}) generated using the program BAMM and which we used to test whether the frequency of migrants in different clades is linearly related to changes in speciation and/or diversification rates (Rabosky et al. 2014; Rabosky and Huang 2016).

3.3.3. Species occurrence data

For each of the migratory and resident species listed in Fishbase, we downloaded all available georeferenced records from the Global Biodiversity Information Facility (GBIF) using the *rgbif* library in R (Chamberlain 2017; R Core Team 2017). This was set to collect all unique records for each species that had coordinates and match these with their taxonomic and life-history data (from Fishbase). First, dubious occurrences were cleaned using the *CoordinateCleaner* library in R, second, minimum and maximum latitude values were extracted for each species, and last we classified the species as "low" latitude if the absolute average <= 30 or 'high" if absolute average >30.

3.3.4. The relationship between speciation rates and migratory life-history traits

Different approaches and methods have been developed to estimate macroevolutionary rates of diversification and to test the dependency of these on different traits. In particular, the Speciation and Extinction (SSE) family of methods, mostly presented in the *diversitree* library

(Fitzjohn 2012) in R, offers several options, that increasing in complexity and depending on data format, fit explicit models to test state-dependent diversification. For example binary data can be tested with Binary State Speciation and Extinction Model (BiSSE), continuous traits with Quantitative State Speciation and Extinction (QuaSSE) and several character state using Multiple States Speciation and Extinction (MuSSE). However, it has been shown that these methods are highly prone to Type-I errors because changes in diversification rates are spuriously associated to variation in character states even when the traits lack a phylogenetic signal (Rabosky and Goldberg 2015). To avoid false positives, one can use the Hidden State Speciation and Extinction (HiSSE) method developed by Beaulieu & O'Meara, (2016) which jointly tests for given character states but also for the presence of a hidden state that could be affecting the diversification process. However, HiSSE only allows to test for one binary trait and given the complexity of our dataset that with several character states, the presence of NA records, and the need to test for latitudinal variation, we used a recently developed method that builds on the previous ones, but additionally allows multiple observed and hidden states, Several Examined and Concealed States-Dependent Speciation and Extinction (SecSSE) (Herrera-Alsina et al. 2018). SecSSE, as HiSSE, allows for concealed states avoiding common Type-I errors, but also allows testing for several character states at the same time. Although SecSSE can handle up to six observed character states at a time, the magnitude of our phylogenetic tree imposed some analytical and time restrictions (long time to compute the ML search). To simplify the analysis and keep the variable parameters to a minimum, we tested for three character states (migratory, resident, anadromous). In more detail, we grouped all species with high dispersion potential as migratory (oceanodromous, amphidromous, potamodromous,

catadromous and brackish), all resident species (marine and freshwater), and anadromous species by themselves, as a preliminary check on their diversification rates showed different patterns from the rest of the migratory species (Fig.1). Additionally, to simultaneously include a second trait (geography) into the analysis, we set latitude to be a function of a "factor". For example, this would mean to say that resident species at low latitudes and resident species at high latitudes have the same basic rate of diversification but they differ by a factor X, which is a number that affects the rate linearly. So, residents-high-latitude species could have a speciation rate which is X times larger than residents-low-latitude species. The X value is optimized by SecSSE but it is the same factor affecting migratory species (i.e., speciation in migratory-high-latitude will also be X times larger than migratory-low-latitude). This set up leads to a total of three different traits to optimize plus one X factor (sampling fractions used are reported in parenthesis): 1. Migratory high latitude (0.78), 2: Anadromous high latitude (0.85), 3: Resident high latitude (0.56), 1X: Migratory low latitude (0.60), 2X: Anadromous low latitude (0.68), 3X: Resident low latitude (0.37).

Using the same scheme established in HiSSE, we denoted observed character states with numbers (1, 2, 3) and concealed character states with letters (A, B, C), and set up three different models of speciation: CR (constant rates) where all species have the same speciation rates ($\lambda_{1A} = \lambda_{2A} = \lambda_{3A} = \lambda_{1B} = \lambda_{2B} = \lambda_{3B} = \lambda_{1C} = \lambda_{2C} = \lambda_{3C}$), CTD (concealed trait dependent) where only the hidden states are allowed to change ($\lambda_{1A} = \lambda_{2A} = \lambda_{3A} \neq \lambda_{1B} = \lambda_{2B} = \lambda_{3B} \neq \lambda_{1C} = \lambda_{2C} = \lambda_{3C}$), and ETD (examined trait dependent) where only the observed state are allowed to change ($\lambda_{1A} = \lambda_{1B} = \lambda_{1C} \neq \lambda_{2A} = \lambda_{2B} = \lambda_{2C} \neq \lambda_{3A} = \lambda_{3B} = \lambda_{3C}$). Additionally, our models specified rates for "biotic exchange" between the different strategies, defined as the likelihood

of transition between migratory, resident and anadromous strategies (specified in Table 1). The ML search was carried out with the simplex algorithm of the *DDD* library in R and, in order to avoid getting caught on a local maximum, we used three sets of initial parameters, resulting in a total of 18 models which were a combination of three models of speciation dependence on traits (CR, CTD and ETD), two evolutionary modes on how the trait evolves over time (constant transitions: only single transition rate for all the shifts; variable transitions: transitions could occur at different rates), three different sets of initial parameters. Selection of the best model was performed using AKAIKE weights (Wagenmakers and Farrel 2004).

3.4. RESULTS

3.4.1. *Phylogenetic and migratory data*

The time tree from Rabosky et al. (2018) contained 11,638 tips (species) of Actinopterygian fishes which included a total of 492 oceanodromous species (sampling fraction, *sf* = 0.68 of the total known diversity in this category); 400 potamodromous (*sf* = 0.69); 115 anadromous (*sf* = 0.66); 69 catadromous (*sf* = 0.82 of the total); 228 amphidromous (*sf* = 0.48); 850 brackish (*sf* = 0.45); 4,120 freshwater (*sf* = 0.28), 4,050 marine (*sf* = 0.28). Supplementary Fig. S1 shows how the different life-history categories for migratory and resident traits divide across 41 Orders and supplemental Fig. S2 shows this distribution across different latitudes.

3.4.2. *Evolutionary rates*

Speciation rates are plotted in Fig. 1. BAMM analysis allows rates to vary during time, therefore it is easier to spot changes in diversification rates that may follow particular events. Generally, between 80-100 MYA during the Late Cretaceous period, all species tended to exhibit an accelerating trend. Fish with an anadromous life-history show the strongest increase in speciation rates, occurring during the last 50-70 MYA. Catadromous and amphidromous fishes increase speciation rates at the lowest pace.

3.4.3. Relationship between speciation rates, migration and latitude

Refer to the panel of Fig. 2A to visualize how different migratory and resident life-history strategies are placed onto the phylogenetic tree. There is no panel for ocean species since these were the main focus of similar research that has already been published (Fig. 3 in Rabosky et al., 2018). Figure 2 shows the relationship of different clades with latitude. In particular, referring to Fig. 2A, several migratory species at high latitudes appear to be part of families undergoing bursts of speciation events. Species among these groups include Salmonidae and Gobidae, which are plastic in their life-history strategies, including representative species in migratory, brackish and freshwater groups (see also Fig. S2). The family of Acipenseridae is also showing high speciation rates at high latitudes, but they are exclusively migratory, including either potamodromous or anadromous species. Within the group of brackish fishes, Fig. 2B, stands out a group of facultative oxygen breathing Perciformes fishes, the Stichaeidae, also known as shannies or pricklebacks, which show high speciation rates at high latitudes. Among the freshwater fishes (Fig. 2C) found with both high rates of speciation and prevalence of habitats at high latitudes, there are several families, such as the Ariidee, Salmonidae, Cottidae, Cyprinodontidae and Poeciliidae. However, the highest speciation rates in freshwater fishes are seen at low latitudes, within clades such as the Cyprinidae (highest speciation rate, lambda = 4.42), Chiclidae, Gobidae and Characidae. Looking at all strategies, in general, freshwater fishes have the highest speciation rates among fish of both northern and southern latitudes, and aside a few exceptions, high rates of speciation in freshwater fishes are mostly evident at low latitudes of the Southern Hemisphere. Highest rates among high latitude

resident fishes are those of ocean fishes in the Southern Hemisphere and the highly plastic Salmoniformes for the Northern Hemisphere, which include freshwater, brackish, and anadromous fishes. Speciation rates are positively correlated with increases in latitude (Fig. 4) only in selected strategies (anadromous R = 0.46, p=value < 0.001; marine R = 0.1, p-value < 0.01; brackish R = 0.1, p-value < 0.001; potamodromous R = 0.15, p-value < 0.01). Freshwater fishes show a weak but significant negative correlation of speciation rate with increasing latitudes (R = -0.098, p-value < 0.001). There are limitations to this analysis as correlations between latitude and speciation rate should be evaluated taking into account phylogenetic dependency (Rabosky et al. 2015; Economo et al. 2019)

3.4.4.   Relationship between speciation rate and percent of migrant in clade

We also asked whether the proportion of migrants within a group has a relationship with the speciation rate of each clade. Fig. 5 A and B report speciation rates and the proportion of migrants at the Family and Order levels, respectively. There is no evidence of a significant relationship in either group (Family, R^2 = 0.0035, p-value = 0.22; Order, R^2 = 0.015, p-value = 0.42). The average speciation rate of most Families of fishes is below 0.5, with just a handful of Families, such as the Chiclidae, Sebastidae, Salmonidae and Artedidraconidae showing higher rates. The Orders with the highest percent of migrants are the Acipenseriformes (100% migratory), Elopiformes (100%), Myctophiformes (~ 70%) and Mugiliformes (~60%).

3.4.5. State-dependent speciation rate

The SecSSE analysis did not find a direct relationship between speciation rates and differences in life-history traits related to dispersal capabilities (migratory, anadromous, residents) (Table 1). The CTD-variable rates model outperformed the rest of the models analyzed. This means that, while there is evidence that the rates between migratory, anadromous and resident fishes are significantly different, these traits are not directly responsible for the differences seen in speciation rates. Additionally, the CTD-variable rates model suggests that speciation rates at low latitudes are approximately twice as high as those of high latitudes (X-factor = 1.87).

3.5. DISCUSSION

This analysis deconstructed the roles of different movement strategies and latitude in influencing the macroevolutionary rates of speciation in fishes. In particular, we hypothesized that the speciation rates of migratory fish species should be different than those of exclusively resident fishes. We used an existing time-calibrated phylogeny of Actinopterygian fishes and tested for state-dependent evolution of traits dependent on movement capabilities and latitude. We found that migrants are different from residents, however, contrary to our hypothesis anadromous and migrating fishes display faster speciation rates. We also found evidence that speciation rates are higher at lower latitudes, as predicted by the DRH. However, we could not confirm whether the specific influence of migratory/resident strategies is driving the observed differences, that is, there is evidence that an additional, concealed trait is driving speciation rates. Additionally, evidence shows that in the Southern Hemisphere faster speciation rates occur at lower latitudes in continental fishes and at higher latitudes in marine fishes, whereas in the Northern Hemisphere anadromous fish prevail at high latitudes and the rest of the fishes are mostly concentrated at lower latitudes with the exception of a few Orders such as the Perciformes and Cypriniformes. There is not clear support to our initial predictions, that is, there is not a clear difference between resident and migratory species with higher diversification rates at high latitudes. In fact, emerging from our results, the most obvious difference, which still remains to be tested as trait-dependent speciation, is that patterns appear

to differ between the Northern and Southern Hemisphere. Most likely, as predicted by the TCH, radiations in continental waters at higher Northern latitudes are still occurring given the relative youth of current temperate habitats; whereas, in the Southern Hemisphere, having less continental areas at higher latitudes probably leads to the lower speciation rates seen in continental-dwelling species.

Lineages through time indicate that rates of diversification are different across strategies, anadromy in particular, but whether each behavior arose independently at different evolutionary times or if each behavioral strategy is exclusive of specific lineages still remains to be explored further.

The taxonomic distribution of migratory fishes is not uniform across the fish phylogeny. That is, there are clades that overall include more migratory species than the rest. For example, more than half of all amphidromous species are comprised within the Order Perciformes, which is the richest Order of ray-finned fishes including over one third of all existing species. According to McDowall (2007), amphidromy is a distinct form of diadromy whereas other authors have described it as a transition between other forms of migratory behavior (Bloom and Lovejoy 2014). Given the ubiquity of the Perciformes fishes and their tendency to display several different life-history movement strategies, transitions between amphidromy, euryhaline brackish water fishes and other migratory and resident strategies could be seen as plasticity inferred by evolutionary adaptations and could be tested in future studies.

In general, migratory strategies can be seen as an evolutionary strategy to avoid extinction and colonize new habitats. These strategies should promote gene flow and decrease

the probability of allopatric speciation. In particular, although we did not include other than ray-finned fishes in this study due to lack of a complete phylogeny, some of the older groups of fishes generally show low species diversity, but high incidence of migratory species. The potamodromous Australian lungfish *Neoceratodus forsteri* (Krefft 1870) is the sole extant member of the Order Ceratodontiformes, while, within the seven species of Pristiformes sawfishes, four are classified as amphidromous and one as oceanodromous. Also, 12 out of 16 of the Lamniformes sharks are oceanodromous, including the Great white shark *Charcharodon carcharias* and the filter-feeding Megamouth shark *Megachasma pelagios* and Basking shark *Cetorhinus maximus*. This may suggest that the migratoriness trait allowed some of these species to persist for million of years despite competition, radiation and establishment of more successful fish species with novel adaptations and higher evolutionary potential. Which are the reasons that could help explain why we are finding higher speciation rates in migratory ray-finned species? It is possible for example, that potamodromous fishes, more vagile than resident freshwater fishes, even if exposed to substantial isolation by vicariance, should experience a higher incidence of speciation events because of their isolation and capacity to reach new environment to colonize. Nevertheless, uncoupling these differences is difficult, since speciation rates are inferred on an incomplete phylogeny and because the link between migratory, resident traits and diversification should be very strong to leave a trace on phylogenies.

Evidence from this work shows that the vagility of migratory species may enhance speciation rates and contribute to sudden bursts in speciation that, as in salmonids, may contribute to colonization of environments, establishment and consequently increases in

species richness. The paradox of diadromous migrations has been discussed by McDowall (2001), who argued that migrations promote gene flow, but at the same time may yield landlocking, isolation and cladogenesis. Migratory fishes have a high potential to invade new, species depauparate zones, become landlocked and possibly go through adaptive radiations (Bamber and Henderson 1988). Once a migratory species gets established in a new environment, species radiations could lead to the accumulation of resident species, which overtime could limit or induce, through density-dependence mechanisms (Fretwell and Lucas 1969; Fretwell 1972), the propensity to migrate. Therefore, both the environment and biotic interactions can lead to the migratory/resident phenotypic plasticity observed in many salmon and trout of the northern hemisphere (Quinn 2005) and galaxiids of the southern hemisphere (Dodson et al. 2009; Górski et al. 2015; Alò et al. 2019). This pattern should be reflected in the diversification of several clades with high proportions of migrants, displaying long stretches of evolutionary stasis, followed by sudden bursts of speciation events.

Several issues further limit the interpretation of our results. In particular, i) the lack of a full species phylogenetic tree; ii) lack of full knowledge on the categorization of migratoriness (i.e. we are not really aware of how many species are truly migratory); iii) lack of full knowledge on actual numbers of extinct species, which impede the calculation of true extinction rates; iv) the association between traits and diversification should be very strong to leave a trace on a phylogeny, in our case, only approximately six percent of species can be categorized as migrants.

This study highlights the importance of migratory fish species in an evolutionary context, as many of these species belong to unique taxa that have withstood the proof of time

throughout a long evolutionary history, such as for example sturgeons, gars and sharks. Protected areas should be designed keeping in mind the life-cycle and extent of movement of these species, as well as the legacy of their evolutionary history. Even if some of these migratory fishes have managed to escape extinction for million of years, habitat fragmentation and global climate warming (e.g. decrease in availability of heterogeneous habitats favored by many migratory species) imposed by the Anthropocene may just be too extreme for many of these fishes.

3.6. SUPPORTING INFORMATION

Figure S1. Dot chart of Order, speciation rate and life-history strategies

Figure S2. Dot chart of Order, midpoint latitude and life-history strategies

CONCLUSIONS

The distribution of life on Earth follows patterns that are dependent on the synergy of ecological and evolutionary processes. The propensity and adaptations that facilitate animal movement can contribute in shaping the biodiversity patterns that we observe today. In this thesis, I worked on different ecological and evolutionary aspects of migratory fishes, attempting to better understand the importance of the environment on their distribution and to assess the evolutionary aspects that differentiate them from sedentary species. In particular, the first chapter reinforced the idea that some geographic areas are more likely then others in favoring the evolution of migratory species. It analyzed otolith microchemistry for native and exotic fishes in Patagonia. Results show that several native species use heterogeneous environment during their life-cycle, and that the migrating behavior of several exotics gets easily established in coastal and inland waters of Chile. This observations support the hypothesis that the biotic and abiotic conditions required to trigger and maintain migrations are present in Chilean waters and further reinforces the important role of heterogeneity and seasonality suggesting that Chile could provide excellent systems to study the evolutionary and ecological adaptations that lead migratory species to colonize new habitats, get established and speciate.

To analyze the role of the environment from a larger perspective, the second chapter analyzed how the environment and phylogenetic diversity interact to influence species

richness of migratory fish species. The relationship of migratory and resident strategies with several environmental variables was analyzed using path analysis and included the influence of phylogenetic diversity. Results show that the different migratory strategies are not evenly distributed around the globe and that migratory fish richness can be explained by the interaction of multiple variables, such as productivity, temperature, environmental heterogeneity, and the role of phylogeny, however these variables interact differentially in each strategy.

To look in more detail at the role of evolution in shaping the current distribution of species, I compared the diversification dynamics of migratory and resident fishes. I found that migrants are different from residents, because of their faster speciation rates and also found that specific clades are most responsible to harbor migratory fish diversity.

Movement is an essential characteristic of the animal kingdom and the specific adaptations that contribute to increase species fitness from its variations have important evolutionary consequences. In particular, the migratory behavior can holistically be seen as a cost-benefit approach (Lack, 1954; Sjaastad, 1962; Borjas, 1987; Gross, 1987; Sword, Lorch, & Gwynne, 2005; Buhl et al., 2006; Railsback & Grimm, 2012; H. Dingle, 2014) dependent on the population influence on the habitat through mechanisms of density-dependence (Fretwell & Lucas, 1969; Fretwell, 1972; H. Dingle, 1980) and the effect of the habitat on the population through seasonality, heterogeneity (Southwood, 1962; Cox, 1968; Winemiller & Jepsen, 1998), availability of resources and energy (Gross, Coleman, & McDowall, 1988; Allen, Brown, & Gillooly, 2002), and very importantly, the role of natural selection to act on the genome of the organisms (H. D. Dingle & Drake, 2007; H. Dingle, 2014) to trigger the

migratory syndrome as a mechanism to avoid extinction (Roff, 1990). Overall, this work supports the interactive role of several hypotheses to elicit the migratory syndrome in animals. Otolith microchemistry has shown that several species in Chilean Patagonia, a heterogeneous and temperate environment, have life cycles consistent with migratory behavior. A multivariate analysis of several abiotic variables influenced by phylogeny helped unveil the complexity of the above-cited interactions and hypotheses. Evolutionary patterns of speciation showed evidence that migratory species have different evolutionary rates compared to resident species and that some migratory lineages are more likely to display a migratory behavior than others. In order to better understand the current distribution of species on Earth and to deconstruct the observed patterns, future research should focus on the roles of evolution, ecology and geology as well as comparing different aspects of species' life-history, which also contributes, with specific adaptations, to shape the species richness observed on our planet.

TABLES

Table 1. Migration deconstructed by factors, levels and processes.
Summarized and merged from the work of different authors (see Alerstam et al. 2003; Dingle and Drake 2007; Börger et al. 2011; Brönmark et al. 2013; Reluga and Shaw 2015)

ORGANISM	POPULATION	FUNCTION	SPACE	TIME	MEDIUM
Obligate **Differential** • Age • Sex	**Facultative** (alternative life-history strategies) **Breeding** **Non-breeding** **Skipped-breeding**	**Spawning** **Refuge from predators** **Adverse environmental conditions** **Feeding**	**To-and-fro** **Round-trip** (Loop, mostly long-lived vertebrates) **One-way** (multigenerational, mostly short-lived organisms) **Vertical** (water depth commuting) **Horizontal** **Altitudinal** **Nomadic**	**Daily** • Nocturnal • Diurnal **Annual** (seasonal) **Irruptive** **Single** (e.g. insects, Pacific salmon, African black oystercatcher) **Periodical** **Synchronized** or **unsynchronized** (zooplankton) **Predictable** (aerobic ciliates) or **unpredictable**	**Terrestrial** **Flight** **Diadromous** (fish & crustaceans) • Catadromy • Anadromy • Amphidromy **Potamodromous** **Oceanodromous** **Passive drift** • Wind • Water Currents • Oxygen sensing

Table 2. **Historical perspective on migration studies**

Main studies that contributed to the development of a "Theory of Migration". While this compilation is not comprehensive of the vast literature available on the subject, it tries to gather the most significant contributions on the theoretical and mathematical consideration analyzed until today to explore the reasons of animal migrations

Type of study (empirical, theoretical, speculative, descriptive)	Organism	Migration Type	Hypothesis	Model	Reference
N/A	Birds	N/A	Northern and southern ancestral home (cited in Cox, 1968; see below)	N/A	Thomson 1926, Lincoln 1939
N/A	Birds	N/A	Leapfrog pattern. (cited in Cox, 1968; see below). Existence of areas with seasonally favorable and unfavorable conditions is required for the evolution of migration.	N/A	Mayr and Meise 1930
Descriptive	Fish	Two-way	Fitness trade-offs	No model, just classification of types of migration in fishes	Myers 1949
Literature Review	Terrestrial arthropods	N/A	Two categories of habitat, "temporary" and "permanent." Within a taxon one should find a higher level of migratory movement in those species associated with temporary habitats than in those with more permanent ones". Spatial & temporal habitat variation. Prime evolutionary advantage of migratory movement lies in its enabling a species to keep pace with the changes in the locations of its habitats	N/A	(Southwood 1962)
Mathematical	Humans	Net migration and Gross migration	Cost-benefit. Migration constitutes a response to spatial earnings differentials. Migration is a search for opportunities in higher-paying occupations.	Interest rate	(Sjaastad 1962)
N/A	Zooplankton	Vertical Migration	Migrating zooplankton may have a metabolic advantage over non-migrating	Estimated an energetic bonus for copepods feeding at night in the warm, food-rich waters and resting in the cold during the day.	(McLaren 1963)

Mathematical	Birds	N/A	Invasion dynamics variation between migrants and residents. Optimal allocation of investments when the returns of the investment are random variables.	Optimal migration fraction	(Cohen 1967)
Theoretical	Mostly birds	Two-way	Density-dependent migrations determined by availability of food on the wintering grounds. For polytypic species (partial migrants) the relative advantages of migration and residency must be nearly equal. Survival value at present time determines whether or not to migrate.	N/A	(Lack 1968)
N/A	Birds	N/A	Migration as metabolic necessity. Cited in Cox 1968. Energy balance as a factor through which advantage could be gained by both northward and southward migration. These studies emphasize the importance of considering bioenergetics in an analysis of the adaptive significance of migration.	N/A	(West 1960; Cox 1961; Zimmerman 1965)
Empirical & Theoretical	Birds	Two-way	State-dependent evolution. Migration created by natural selection. Rate of reproduction should be higher in residents. Resident behavior favored by choice of territory and nesting-places and increased chances of finding mates (reach reproductive maturity earlier). Selection through differential mortality (higher in residents) maintains migration strategies.	N/A	(von Haartman 1968)
Theoretical and Graphical with empirical data	Birds	N/A	Migration is the normal evolutionary consequence, for highly mobile animals, of intra- & interspecific competition as selective agents operating in a seasonal environment	N/A	(Cox 1968)
N/A	Anadromous fish	Obligate	Genetically determined migration, shown that differences in migratory behavior are genetically-determined and are largely considered to be constitutively-expressed as obligate strategies	N/A	Gwinner 1969
Theoretical and Graphical models	N/A	N/A	Theory of ideal free distribution or density dependent habitat selection (IFD/DDHS) link individual choices to the distribution of populations.	N/A	(Fretwell and Lucas 1969)

N/A	Birds	N/A	Competition based origin of migration	N/A	(Fretwell 1972)
Theoretical	Zooplankton	N/A	Demographic advantage of migrating zooplankton	N/A	McLaren 1974
N/A	N/A	N/A	For many different climates and groups of organisms the total number of species in a small region is given by: St = A ln (1 + B/1) where q is a measure of environmental fluctuation (e.g. temperature range) whilst A and B are constants for the area in question (found by a least-squares fit). Their exact biological meaning is unclear, but B seems to be a measure of the range of resources available and A expressed various biogeographical conditions-rates of introduction, speciation and establishment and the 'equilibrium number'. In the terms in which I have defined this axis, B is clearly related to r, whilst t, is a measure of V. (taken from Southwood 1977)	N/A	MacArthur 1975
Theoretical and Graphical models	General	N/A	Migrants occupy ephemeral habitats. Optimal strategy, multi-dimensional models that include various habitat characteristics that influence reproductive success	H/τ where H = length of time the habitat remains favorable and r = generation time. When this ratio approaches unity a migration strategy is favored	(Southwood 1977)
Empirical and Graphical models	Birds	N/A	Strong effect of latitude in Europe	Used multivariate regression models to examine the proportion of migrants in various communities as a function of different combinations of geographic and climatic variables. The best single predictor was latitude followed by temperature of the coldest month. Harshness of winter coupled with total resources available during breeding best explains the proportion of migrants.	Herrera 1978
N/A	Birds	N/A	(1) What makes the fitness of a bird higher if it migrates? and (2) Why do some birds migrate while others do not? (Fretwell, 1978) Competition based origin of migration. Cited in Dingle 1980… see below	N/A	Fretwell 1978

Theoretical Review	Multispecies	N/A	Migrants as "fugitives"; Selection for migration seems to center on the balance between food availability and heat loss	Migratory species tend to be "r-strategists" rather than "K-strategists" in life history terminology (e.g., Stearns, 1976) and to show high intrinsic rates of increase (r).	(Dingle 1980)
Empirical	Birds	N/A	Genetically determined migration	N/A	(Berthold and Querner 1981)
Theoretical	N/A	N/A	The theory of games, first developed to analyze economic behavior, is modified so that it can be applied to evolving populations. John Maynard Smith's concept of an evolutionarily stable strategy is relevant whenever the best thing for an animal or plant to do depends on what others are doing. The theory leads to testable predictions about the evolution of behavior, of sex and genetic systems, and of growth and life history patterns.	N/A	(Maynard Smith 1982)
N/A	Ungulates	N/A	Seasonal variation encourages migration	N/A	Sinclair 1983
Theoretical, Mathematical and Empirical	Humans	N/A	Cost-Benefit	There are three possible scenarios with respect to migrants' self-selection: positive selection, where migrants earn above average wages in both countries; negative selection, where migrants are drawn from the left tail of the income distribution, and underperform the natives at destination; 3 refugee sorting, where migrants are drawn from the left tail of the income distribution, but outperform natives at destination	(Borjas 1987)
N/A	Fish	Diadromous	Fitness trade-offs	Yes	(Gross 1987)
Theoretical	Fish	Diadromous	Productivity drives diadromy in fishes	N/A	(Gross et al. 1988)

Graphical model	Birds	N/A	Migration as ESS. Condition- dependence and frequency-dependence play a role in the regulation of partial migration in birds	If the system is a mixed ESS at the individual level, no genetic determination should be found. Choice of tactics should be purely stochastic, finally adjusted so that the equilibrium frequencies are maintained.	(Lundberg 1987)
Theoretical & Graphical model	Large Herbivores	Two-way	Migrants are less vulnerable to predation.1.Seasonal variation and predator avoidance encourages migration. 2.Residents may be more prone to regulation at low densities by predation, while migrants are more likely to be regulated by competition for food resources.	Seasonal and spatial variations in food quality appear to be generally more important than absolute abundance in selecting for migratory behavior.	(Fryxell and Sinclair 1988)
N/A	Salmon	Anadromous	Fitness trade-offs	N/A	Thorpe 1988,
Review	Zooplankton	Vertical Migration	Favors: "better hungry than dead", predator-avoidance theory.	N/A	(Lampert 1989)
N/A	N/A	N/A	Spatial & temporal habitat variation	N/A	Dingle 1989
Theoretical Review and Empirical work	N/A	N/A	Spatial & temporal habitat variation. Importance of habitat heterogeneity. "Flightlessness will most likely evolve in circumstances where movement on a large scale is not required, i.e. in a spatially homogenous and temporally stable environment".	Migration can have significant effects on the persistence of a species. However it is costly because many migrants fail to find new habitats and because it is energetically expensive and reduces fecundity or mating success.	(Roff 1990)
N/A	Birds	N/A	Different approach from the cost-benefit analysis. They ask if specific ecological traits make some species more likely to be long-distance than others.	N/A	Levey and Stiles 1992
Mathematical	Birds	Partial	Model of Partial Migration as ESS based on the stability properties of dynamic systems. t derive a concept of an ESS that is based on the stationary distribution of populations playing various strategies and on the expected success of invasion by a mutant strategy. They show that environmental variability is not a prerequisite for partial migration and suggest that future studies should focus on density-dependent and independent mortality patterns and differential	Population dynamics model	(Kaitala et al. 1993)

			reproductive success among migrants and residents.		
N/A	Salmon	Anadromous	Fitness trade-offs	N/A	Økland et al 1993
Mathematical	Salmonids	Anadromous	Construct a model of a "General Salmonid" by capturing the salient biological properties of salmon and predict the effects of climate change on their migratory behaviour	Effects of climate change on salmon patterns of development and maturation. Main variables are weight and length of the fish (related by allometric growth), the metabolic rate and environmental properties such as food availability and water temperature.	(Mangel 1994)
N/A	Birds	N/A	"The phenotypic dichotomy "migrant-non migrant is caused by a threshold which may not be fixed but influenced both genetically and environmentally.	Threshold model of Quantitative genetics. The model assumes that there is an unknown continuously distributed variable (=liability) underlying the dichotomous trait of migration/residency. Selection could either shift the populational mean of liability (22, 23) or could change the position of the individual threshold (26)	(Pulido et al. 1996)
Review	Multispecies	N/A	Migratory syndrome. Fitness changes as a result of migratory behavior. Spatial & temporal habitat variation. Affirms that diadromy is sufficiently different from other migratory systems that require its own conceptual description and analysis.	Summarizes (Roff 1990, 1994), in a heterogeneous environment migration will evolve as a function of the cost of migration, the number of habitat patches, and the means and variances of X and K	Dingle 1996
N/A	Salmon	Diadromy	Relate migratory behavior to reproductive success in fishes. "The evolution of fish migration may best be understood by considering the fitness benefits that accrue to individuals who migrate to and exploit specific reproductive habitats, as well as the fitness benefits that accrue to fish following their emigration from the reproductive habitat. States that diadromy may have evolved to improve fitness by improving survival of the early-life history stages rather than by improving the	Discusses the shortcomings of Gross' productivity hypothesis	(Dodson 1997)

			growth of older fish. Selection should favor the evolution of behavioral traits that minimize energetic expenditures.		
N/A	Anadromous fish	Obligate	Genetically determined migration	N/A	Widmer 1999
N/A	Shorebirds	N/A	Vicariance biogeography and phylogeny to explain patterns of seasonal migration. Seasonal variation encourages migration. Not very relevant for my discussion…	Treat breeding and non-breeding distributions as characters with the continent or continental region of these distributions as the character states, and then investigate the direction of change in these characters when mapped onto an independently derived phylogeny	(Joseph et al. 1999)
Mathematical, Theoretical, Graphical	Birds	N/A	Proposes "alternative model" that is migration first appears as a temporary directional shift away from the breeding site outside the reproductive period, in response to seasonal variation in the direction and/or severity of environmental gradients across the range of a sedentary population.	Transition from resident to long-distance migrant emerges as a three-stage process, starting with the origin of the migratory habit, followed by establishment of fully migratory populations and ending with the disappearance of ancestral resident populations. I like his definition of migration: "Migration may be defined as a periodic cyclical movement of the center of activity, the path of which is to some extent heritable"	(Bell 2000)
Mathematical, Theoretical, Graphical	Birds	N/A	Show that migration can be an ESS only if year-round residency in a given area would produce a sink population, where mortality exceeds reproduction.	"Competition for limited breeding sites could thus favor year-round residency". "Two potential benefits of nonresidency: first, the nonresident may find a better breeding site than it was inhabiting before, and second, it may survive better than a resident, particularly if nonresidency permits migration to an overwintering area.	(Kokko and Lundberg 2001)

Empirical, Theoretical, Mathematical	Thomson's gazelles	N/A	Linked behavioral modeling with observational studies to predict spatial distribution	Population-level approach	(Fryxell et al. 2004)
Experimental	Crickets	N/A	Fitness trade-offs. Aggregation and constant movement protect band members from predators while reducing costs due to competition for resources and cannibalism.	N/A	(Sword et al. 2005)
Experimental	Crickets	N/A	Fitness trade-offs. Migratory band formation and subsequent mass movement, therefore, are manifestations of specific tradeoffs between the costs and benefits of group living. Bands afford antipredator benefits to individual group members. Group movement then mitigates the resulting costs of intraspecific competition, namely local depletion of nutritional resources and the associated increased risk of cannibalism.	Protein satiety inhibits locomotion.	(Simpson et al. 2006)
Theoretical and Graphical with empirical data	Wildebeest	N/A	Evolutionary programming to simulate emergence of alternative migration routes	Population-level approach.	(Boone et al. 2006)
Theoretical Review	Birds	N/A	Environmentally triggered genetic variation. Review how our evolutionary understanding of migration may benefit from taking a quantitative-genetic approach and present a framework for studying the causes of phenotypic variation.	We can observe phenotypes and variances in trait values. This variance can be split into components due to known variation in environmental conditions, error variation due to uncontrolled or unknown environmental variation, genetic variation in the average phenotype, and genotype–environment interaction, i.e. differences in reaction norms among genotypes.	(van Noordwijk et al. 2006)
Experimental	Locusts	N/A	Density-dependent migrations. Find critical density at which marching locusts would spontaneously and suddenly adopt directed collective motion.	N/A	(Buhl et al. 2006)

Review	Birds	N/A	Threshold model of expression of migratory behavior in partial migrants. Some general features are common to all migratory individuals--for instance, the suppression of maintenance activities or the deposition. Good review on evolution of migration and different questions related to it. "The colonization of new areas seems to have been the most important selective factor for the de novo evolution of migration or its loss in a lineage" citation of Joseph et al 2003; Outlaw and Voelker 2006	Genetic variation of migratory traits	(Pulido 2007)
Empirical	Birds	N/A	New hypothesis for migration emergence: the 'shifting home model'. It considers climatic zone shifts as primary driver.	Reviewed and compared fossil bird distribution evidence and paleoclimatic Cenozoic data relative to tropical biome limits and evolution of seasonality (quantified winter and summer climatic parameters).	(Louchart 2008)
Mathematical	Birds	N/A	Seasonal variation encourages migration.	Annual routine model of migration	(Barta et al. 2008)
N/A	Multispecies	N/A	"Movement ecology"	Proposes a unifying paradigm termed movement ecology for studying movements of organisms of all kinds.	(Nathan et al. 2008)
Conceptual framework	N/A	N/A	Contribute to a synthesis of "movement ecology" by outlining an integrative, conceptual framework encompassing many of the various movement types that animals usually exhibit	Combined Individual-based with Population-level approach	(Mueller and Fagan 2008)
Conceptual model	Cyprinids	N/A	Fitness trade-offs	Hypothesized that migration is an adaptive behavior in response to seasonal changes in predation (P) and growth (G) and that migrating fish change habitat so as to minimize the ratio between predation mortality and growth rate (P/G).	Brönmark et al 2008
Integrated experimental and theoretical approach	Locusts	N/A	Density-dependent migrations. Investigate directional switching in a Self Propelled Particle model and in experimental data of the motion of locusts determine the mean time between direction switches as a function of group density	Individual-based model	(Yates et al. 2009)

			for the experimental data and the self-propelled particle model.		
Theoretical approach	Locusts	N/A	Coordinated mass migration.	Individual based model of Brownian particles interacting by pursuit and escape interactions for the kinematic description of large groups of individuals, where each individual respond to others in itslocal neighborhood by escape and pursuit behavior. The response itself is described by effective social force acting on each individual and is motivated by recent experimental results on mass migrating insects.	(Romanczuk et al. 2008)
Review	Locusts	N/A	Density-dependent color change, gregariousness and migratory syndrome. Phase polyphenism in locusts is related to extreme fluctuations in population size and the probability of swarm formation. The observed correlation between phase polyphenism and propensity of locusts to swarm led to the idea that phase change is an adaptation for migration in the face of environmental heterogeneity. Many density dependent phase traits can be interpreted in terms of their value as migratory adaptations. However, populations of gregarious phase locusts do not necessarily swarm and solitarious phase locusts also migrate, but not en masse.	N/A	(Simpson and Sword 2009)
N/A	N/A	N/A	Density-dependent migrations	Population-level approach	Holdo et al 2009
Theoretical Review	Multispecies	N/A	Fission-Fusion dynamics	Individual-based model	Couzin and Laidre 2009
Integrated experimental and theoretical approach	Steelhead *Oncorhynchus mykiss*	N/A	Changes in growth rate driven by climate change migratory behavior	Combine physiological and expected reproductive success to find a threshold spike for emigration in *O. mykiss* (Steelhead)	(Satterthwaite et al. 2009)

Integrated experimental and theoretical approach	Locusts	N/A	Fitness trade-offs. Explore how the internal state—in particular the nutritional state—of an individual locust affects its motion. Then consider the interactive effects of internal state and external factors, namely social cues from conspecifics, on individual motion.	An experimentally parameterized model of locust interactions and motion. Use the probabilistic nature of movement to both gain insight into experimental data and to develop a model of individual and collective motion using an individual-based approach	(Bazazi et al. 2011)
N/A	Multispecies	N/A	Linkage of genetic and demographic dynamics	Evolutionary invasion analysis (calculates whether a new mutation will spread in a population). Model for the evolution of migration in a seasonal environment that incorporates genetic, ecological and demographic information.	(Griswold et al. 2010)
Theoretical	General model	N/A	Mixed ESS in seasonal habitats	N/A	(Holt and Fryxell 2011)
Theoretical and Mathematical	Birds	N/A	1.The evolutionary solution to the partial migration game is not necessarily an ESS. 2. Individual-based evolutionary solution deviates from the optimal solution for the population. 3.Partial migration is unlikely to evolve without frequency- or density-dependent selection.	N/A	(Lundberg 2013)
Theoretical	Multispecies	N/A	Outline general patterns to explain migration in all taxa	N/A	(Dingle and Drake 2007; Dingle 2014)

Table 3. Description of the samples studied and summary of results of migration pattern determination.
Values correspond to the percentage of individuals assigned to one of five possible patterns: freshwater resident (FW), brackish water resident (B), anadromous (ANA), catadromous (CAT), amphidromous (AMPH) or else omitted from interpretation due to uncertainties in the otolith transects (O).

| | Species | N | Location | Year | Latitude | Longitude | Inferred Migratory Strategy (%) | | | | | |
							FW	B	ANA	CAT	AMPH	O
Native Galaxiids	*A. zebra* (Jenyns, 1842)	5	Aysén-Caro	2009	-45.80	-72.55	100					
	A. zebra	3	Chiloé-Tocoihue	2011	-42.30	-73.44		100				
	A. taeniatus (Eigenmann, 1928)	8	Valdivia-Santo Domingo	2010	-39.91	-73.14		12.5		50	25	12.5
	A. taeniatus	2	Valdivia-Lingue	2011	-39.46	-73.09				100		
	A. taeniatus	3	Aysén-Palos	2007	-45.32	-72.70				66.7		33.3
	A. taeniatus	2	Aysén-Caro	2009	-45.80	-72.55	100					
	A. marinus (Jenyns, 1842)	7	Baker-estuary	2007	-47.79	-73.52				100		
	G. platei (Steindachner, 1898)	2	Aysén-Palos	2007	-45.32	-72.70	100					
	G. maculatus (Jenyns, 1842)	4	Chiloé-Tocoihue	2011	-42.30	-73.44		25		50	25	
Introduced Salmonids	*S. trutta* (Linnaeus, 1758)	4	Aysén-Palos	2007	-45.32	-72.70	100					
	S. trutta	4	Aysén-Caro	2009	-45.80	-72.55	100					
	S. trutta	1	Baker-estuary	2007	-47.79	-73.52			100			
	O. tshawytscha (Walbaum, 1792)	8	Aysén-Ñireguao	2004	-45.17	-72.12			75			25
	O. tshawytscha	8	Baker-Jaramillo	2004	-47.70	-73.05	12.5		50			37.5
	O. tshawytscha	6	Petrohué-Patos	2004	-41.18	-72.46			66.7			33.3
	O. tshawytscha	4	Toltén-Peuco	2004	-38.85	-71.76			50			50
	O. tshawytscha	4	Toltén-Truful	2004	-38.85	-71.67			50			50
	O. tshawytscha	5	Aysén-Simpson	2008	-45.73	-72.10	80					20
	O. kisutch (Walbaum, 1792)	2	Baker-Vargas	2007	-47.68	-73.04			100			
	O. mykiss (Walbaum, 1792)	3	Aysén-Caro	2009	-45.80	-72.55	100					

Table 4. Migratory life-histories and hotspot summaries.
The total species richness according to Fishbase and Raw and Cleaned occurrences downloaded from GBIF. SR Hotspot lists the three ecoregions with the highest species richness for each migratory category and their associated realms and provinces (except for purely freshwater ecoregions). Layers indicate freshwater (FEOW) (Abell et al. 2008b) and/or marine (MEOW)(Spalding et al. 2007) ecoregions or pelagic provinces (PPOW)(Spalding et al. 2012) of the world.

Migratory Life-history	N	Raw occurrences	Cleaned occurrences	SR Hotspot (N)	Realm	Province	Layers
Amphidromous	401	310,420	186,143	Eastern Philippines (99)	Central Indo-Pacific	Western Coral Triangle	MEOW/FEOW
				Southern China (83)	Central Indo-Pacific	South China Sea	MEOW/FEOW
				Arnhem Coast to Gulf of Carpentaria (79)	Central Indo-Pacific	Sahul Shelf	MEOW
Anadromous	140	452,056	261,338	Gulf of St. Lawrence Coastal Drainages (24)			FEOW
				Northern California (22)	Temperate Northern Pacific	Cold Temperate Northeast Pacific	MEOW/FEOW
				Virginia (22)	Temperate Northern Atlantic	Cold Temperate Northwest Atlantic	MEOW/FEOW
				Eastern Bering Sea (22)	Arctic	Arctic	MEOW/FEOW
Catadromous	81	146,577	102,262	Natal (19)	Temperate Southern Africa	Agulhas	MEOW/FEOW
				Arnhem Coast to Gulf of Carpentaria (19)	Central Indo-Pacific	Sahul Shelf	MEOW
				Bismarck Sea (18)	Central Indo-Pacific	Eastern Coral Triangle	MEOW/FEOW
Oceanodromous	646	1,445,928	1,064,568	Transitional biome (239)	Indo-Pacific Warm Water	Non-gyral Southwest Pacific	PPOW
				Boundary-western biome (216)	Atlantic Warm Water	Gulf Stream	PPOW
				Gyre biome (196)	Indo-Pacific Warm Water	South Central Pacific gyre	PPOW
Potamodromous	531	486,631	305,275	Gulf of Tonkin (97)	Central Indo-Pacific	South China Sea	MEOW/FEOW
				Polar biome (95)	Northern Cold Water	Arctic	PPOW
				Volta (93)			FEOW
Ocean resident	1125	786,161	690,073	Transitional biome (143)	Indo-Pacific Warm Water	Non-gyral Southwest Pacific	PPOW
				Exmouth to Broome (140)	Central Indo-Pacific	Northwest Australian shelf	MEOW
				Eastern Philippines (137)	Central Indo-Pacific	Western Coral Triangle	MEOW
Freshwater resident	1476	167,419	134,245	Amazonas Lowlands (141)			FEOW
				Río Negro basin (83)			FEOW
				Northern Philippines Islands (137)	Central Indo-Pacific	Western Coral Triangle	MEOW/FEOW

Table 5. Latent and manifest variables tested.
Rows in bold indicate which were the best variables ultimately chosen to be included in the models. Support to include a manifest variable in the model was provided by its unidimensionality values in the partial least square approach algorithm executed in path analysis (Sanchez 2013). The "category" column specifies for which migratory/resident strategy each manifest variable was used.

Latent Variable	Manifest variable	Description	Category	Unit	Source	Reference
TEMPERATURE	temp/BIO1	Land average annual temperature in celsius	ANA, CAT, AMP, POT, FW RES	Celsius	WorldClim version 2.0	Fick & Hijmans, 2017
PRODUCTIVITY	**npp**	**Land average annual productivity**	**ANA, CAT, AMP, POT, FW RES**	**gC/m2/ye ar**	**MODIS17A3, Earth Observing System (NASA)**	**Zhao et al., 2005**
HETEROGENEITY	BIO2	mean diurnal range	ANA, CAT, AMP, POT, FW RES	Celsius	WorldClim version 2.0	Fick & Hijmans, 2017
HETEROGENEITY	BIO3	isothermality	ANA, CAT, AMP, POT, FW RES	Celsius	WorldClim version 2.0	Fick & Hijmans, 2017
HETEROGENEITY	**BIO4**	**temperature seasonality**	**ANA, CAT, AMP, POT, FW RES**	**Celsius**	**WorldClim version 2.0**	**Fick & Hijmans, 2017**
TEMPERATURE	**BIO5**	**max temperature of warmest month**	**ANA, CAT, AMP, POT, FW RES**	**Celsius**	**WorldClim version 2.0**	**Fick & Hijmans, 2017**
TEMPERATURE	**BIO6**	**min temperature coldest month**	**ANA, CAT, AMP, POT, FW RES**	**Celsius**	**WorldClim version 2.0**	**Fick & Hijmans, 2017**
HETEROGENEITY	**BIO7**	**temperature annual range**	**ANA, CAT, AMP, POT, FW RES**	**Celsius**	**WorldClim version 2.0**	**Fick & Hijmans, 2017**
TEMPERATURE	**BIO8**	**mean temperature of wettest quarter**	**ANA, CAT, AMP, POT, FW RES**	**Celsius**	**WorldClim version 2.0**	**Fick & Hijmans, 2017**
TEMPERATURE	**BIO9**	**mean temperature of driest quarter**	**ANA, CAT, AMP, POT, FW RES**	**Celsius**	**WorldClim version 2.0**	**Fick & Hijmans, 2017**
TEMPERATURE	**BIO10**	**mean temperature of warmest quarter**	**ANA, CAT, AMP, POT, FW RES**	**Celsius**	**WorldClim version 2.0**	**Fick & Hijmans, 2017**
TEMPERATURE	**BIO11**	**mean temperature of coldest quarter**	**ANA, CAT, AMP, POT, FW RES**	**Celsius**	**WorldClim version 2.0**	**Fick & Hijmans, 2017**
PRECIPITATION	**BIO12**	**annual precipitation**	**ANA, CAT, AMP, POT, FW RES**	**mm**	**WorldClim version 2.0**	**Fick & Hijmans, 2017**

PRECIPITATION	BIO13	precipitation of wettest month	ANA, CAT, AMP, POT, FW RES	**mm**	WorldClim version 2.0	Fick & Hijmans, 2017
PRECIPITATION	**BIO14**	**precipitation of driest month**	**ANA, CAT, AMP, POT, FW RES**	mm	**WorldClim version 2.0**	**Fick & Hijmans, 2017**
HETEROGENEITY	BIO15	precipitation seasonality	ANA, CAT, AMP, POT, FW RES	**mm**	WorldClim version 2.0	Fick & Hijmans, 2017
PRECIPITATION	BIO16	precipitation of wettest quarter	ANA, CAT, AMP, POT, FW RES	**mm**	WorldClim version 2.0	Fick & Hijmans, 2017
PRECIPITATION	**BIO17**	**precipitation of driest quarter**	**ANA, CAT, AMP, POT, FW RES**	mm	**WorldClim version 2.0**	**Fick & Hijmans, 2017**
PRECIPITATION	**BIO18**	**precipitation of warmest quarter**	**ANA, CAT, AMP, POT, FW RES**	mm	**WorldClim version 2.0**	**Fick & Hijmans, 2017**
PRECIPITATION	**BIO19**	**precipitation of coldest quarter**	**ANA, CAT, AMP, POT, FW RES**	mm	**WorldClim version 2.0**	**Fick & Hijmans, 2017**
TEMPERATURE	**temp**	**Ocean average annual temperature**	**OCE, OCE RES**	**Celsius**	**AquaMaps Environmental Dataset**	**Kaschner et al., 2008**
PRODUCTIVITY	**npp**	**Ocean average net primary productivity**	**OCE, OCE RES**	**gC/m2/year**	**MODIS-Aqua product, Ocean Productivity site**	**Behrenfeld and Falkowski 1997a**
PRODUCTIVITY	cal	calcite	**OCE, OCE RES**	mol.m-3	Bio-ORACLE version 2.0	Assis et al., 2017
PRODUCTIVITY	chl	chlorophyll	OCE, OCE RES	mg.m-3	Bio-ORACLE version 2.0	Assis et al., 2017
HETEROGENEITY	clo	cloud cover	OCE, OCE RES	%	Bio-ORACLE version 2.0	Assis et al., 2017
HETEROGENEITY	vel	current velocity	OCE, OCE RES	m-1	Bio-ORACLE version 2.0	Assis et al., 2017
PRODUCTIVITY	da	diffuse attenuation	OCE, OCE RES	m-1	Bio-ORACLE version 2.0	Assis et al., 2017
PRODUCTIVITY	dox	dissolved oxygen	OCE, OCE RES	mol.m-3	Bio-ORACLE	Assis et al., 2017

					version 2.0	
HETEROGENEITY	**icec**	**ice cover**	**OCE, OCE RES**	**proportion**	**Bio-ORACLE version 2.0**	**Assis et al., 2017**
HETEROGENEITY	**icet**	**ice thickness**	**OCE, OCE RES**	**m**	**Bio-ORACLE version 2.0**	**Assis et al., 2017**
PRODUCTIVITY	iron	iron	OCE, OCE RES	umol.m-3	Bio-ORACLE version 2.0	Assis et al., 2017
PRODUCTIVITY	nit	nitrate	OCE, OCE RES	mol.m-3	Bio-ORACLE version 2.0	Assis et al., 2017
PRODUCTIVITY	par	photosyntethically active radiation	OCE, OCE RES	E.m-2.day-1	Bio-ORACLE version 2.0	Assis et al., 2017
PRODUCTIVITY	Ph	phosphate	OCE, OCE RES	mol.m-3	Bio-ORACLE version 2.0	Assis et al., 2017
PRODUCTIVITY	phy	phytoplankton	OCE, OCE RES	umol.m-3	Bio-ORACLE version 2.0	Assis et al., 2017
TEMPERATURE	sal	salinity	OCE, OCE RES	PSS	Bio-ORACLE version 2.0	Assis et al., 2017
PRODUCTIVITY	sil	silicate	OCE, OCE RES	mol.m-3	Bio-ORACLE version 2.0	Assis et al., 2017
PHYLOGENETIC STRUCTURE	**PCPS**	**Phylogenetic filters**	**All**	**proportion**	**This study**	
RICHNESS	**sr**	**species richness per grid cell**	**All**	**number**	**This study**	

Table 6. Relationship between productivity and species richness (PSRR).
Columns 2-5 report results of the fit of the generalized linear model (GLIM) with assumption of Poisson error distribution and logarithmic link function using the equation: species richness = a + b(productivity) + c(productivity)^2 (Mittelbach et al. 2001). Mitchell-Olds and Shaw test (MOStest) was used to assess the significance of the quadratic component with the null hypothesis that the hump of the quadratic coefficient is at a minimum or a maximum (Leibold 1999; Mittelbach et al. 2001). n/a: test not applicable because non-significance of the quadratic component was determined in GLIM

	GLIM(poisson, link=log)				MOStest		
Strategy	**quad coef**	**quad p value**	**linear coef**	**lin p value**	**min p-value**	**max p-value**	**Pattern**
Anadromy	-2.00E-06	1.30E-12	0.0026	6.60E-16	2.00E-54	1.50E-14	Hump
Catadromy	-6.00E-07	0.0047	0.0017	3.60E-07	4.90E-06	0.21	Positive
Amphidromy	-1.30E-07	0.3700	0.0010	4.90E-06	n/a	n/a	Positive
Potamodromy	-7.60E-07	4.5E-06	0.0014	4.30E-08	8.30E-09	2.60E-05	Hump
Oceanodromy	-3.10E-07	0.0024	7.90E-04	5.60E-11	4.50E-11	0.21	Positive
Ocean Residency	-1.40E-07	0.1900	7.70E-04	3.00E-07	n/a	n/a	Positive
FW residency	-2.10E-07	0.0280	9.40E-04	2.50E-11	7.10E-12	0.90	Positive

Table 7. Summary of the relationship between diversity and temperature.
 Relationship between diversity and temperature for each of the life-history strategies of fish illustrated in Fig. 9. P-value column significant codes: n/a, not reported.

Group	Slope	2.5% CI	97.5% CI	Intercept	r	p-value	n	Dataset
Riverine Fish	-9.16	-11.09	-7.66	35.55	0.43	n/a	165	Allen et al 2002
Anadromy	-2	-4.49	0.48	9.87	0.09	0.11	151	This study
Catadromy	-5.86	-7.182733	-4.54	23.18	0.77	<0.001	81	This study
Amphidromy	-11.1	-12.1	-10.11	42.35	0.95	<0.001	425	This study
Potamodromy	-6.47	-8.7	-4.25	26.48	0.62	<0.001	545	This study
Oceanodromy	-6.85	-8.23	-5.47	28.98	0.75	<0.001	711	This study
Ocean residents	-10.34	-11.88	-8.8	40.9	0.86	<0.001	1125	This study
Freshwater residents	-9.7	-11.27	-8.12	38.4	0.85	<0.001	1476	This study
All	-9.11	-10.52	-7.7	37.95	0.83	<0.001	4514	This study

Table 8. Summary of the Several Examined and Concealed States-Dependent Speciation and Extinction (SecSSE) models.
A total of six models with variable and constant rates and different evolutionary models were run (Constant rates (CR), Examined Trait Dependent (ETD) and Concealed Trait Dependent). For each of these, three replicas with different initial parameters were run, with a total of 18 models. Herein only the group of replicas with the best Akaike values are reported. The model in bold is the best model as defined by its Akaike weight. Speciation rate, Lambda (λ), extinction rate, Mu (μ), and transition rates (q) are reported only for the high latitude models. To obtain values for the low latitude models, high latitude values should be multiplied by the X-factor, if the X-factor $\approx$ 1, then there is no real difference between low and high latitude in the model proposed. "np" is the number of parameters evaluated in each model.

Models	Migratory λ0	Anadromy λ1	Resident λ2	μ0	q01	q10	q02	q20	q12	q21	lnLik	np	AICw	X-factor
CR λ1A=λ2A=λ3A=λ1B=λ2B=λ3B=λ1C=λ2C=λ3C; q01 = q10; q02 = q20, q12 = q21	0.1325	0.1325	0.1325	0.0847	0.0033	0.0033	0.0033	0.0033	0.0033	0.0033	-53528.37	3	0.00	1.00
CR λ1A=λ2A=λ3A=λ1B=λ2B=λ3B=λ1C=λ2C=λ3C; q01 = q10; q02 ≠ q20, q12 ≠ q21	0.1306	0.1306	0.1306	0.0825	0.0004	0.0004	0.0284	0.0020	0.0284	0.0020	-52816.46	6	0.00	1.00
ETD λ1A=λ1B=λ1C≠λ2A=λ2B=λ2C≠ λ3A=λ3B=λ3C; q01 = q10; q02 = q20, q12 = q21	0.1018	0.0212	0.1421	0.0854	0.0043	0.0043	0.0043	0.0043	0.0043	0.0043	-53045.13	6	0.00	1.02
ETD λ1A=λ1B=λ1C≠λ2A=λ2B=λ2C≠ λ3A=λ3B=λ3C; q01 = q10; q02 ≠ q20, q12 ≠ q21	0.1113	0.0641	0.1320	0.0708	0.0006	0.0006	0.0217	0.0028	0.0217	0.0028	-52733.79	9	0.00	0.98
CTD λ1A=λ2A=λ3A≠λ1B=λ2B=λ3B≠λ1C=λ2C=λ3C; q01 = q10; q02 = q20, q12 = q21	0.0556	0.1788	0.0256	0.0000	0.0028	0.0028	0.0028	0.0028	0.0028	0.0028	-51812.62	6	0.00	1.90
CTD λ1A=λ2A=λ3A≠λ1B=λ2B=λ3B≠λ1C=λ2C=λ3C; q01 = q10; q02 ≠ q20, q12 ≠ q21	**0.0668**	**0.1920**	**0.0165**	**0.0001**	**0.0004**	**0.0004**	**0.0260**	**0.0017**	**0.0260**	**0.0017**	**-50723.69**	**9**	**1.00**	**1.87**

FIGURES

Figure 1. Diadromy explained.
Visualization of the different patterns of diadromy to explain how anadromous, catadromous and amphidromous species rely on feeding and reproduction to time different life-history events moving between freshwater and the sea (from McDowall 1997).
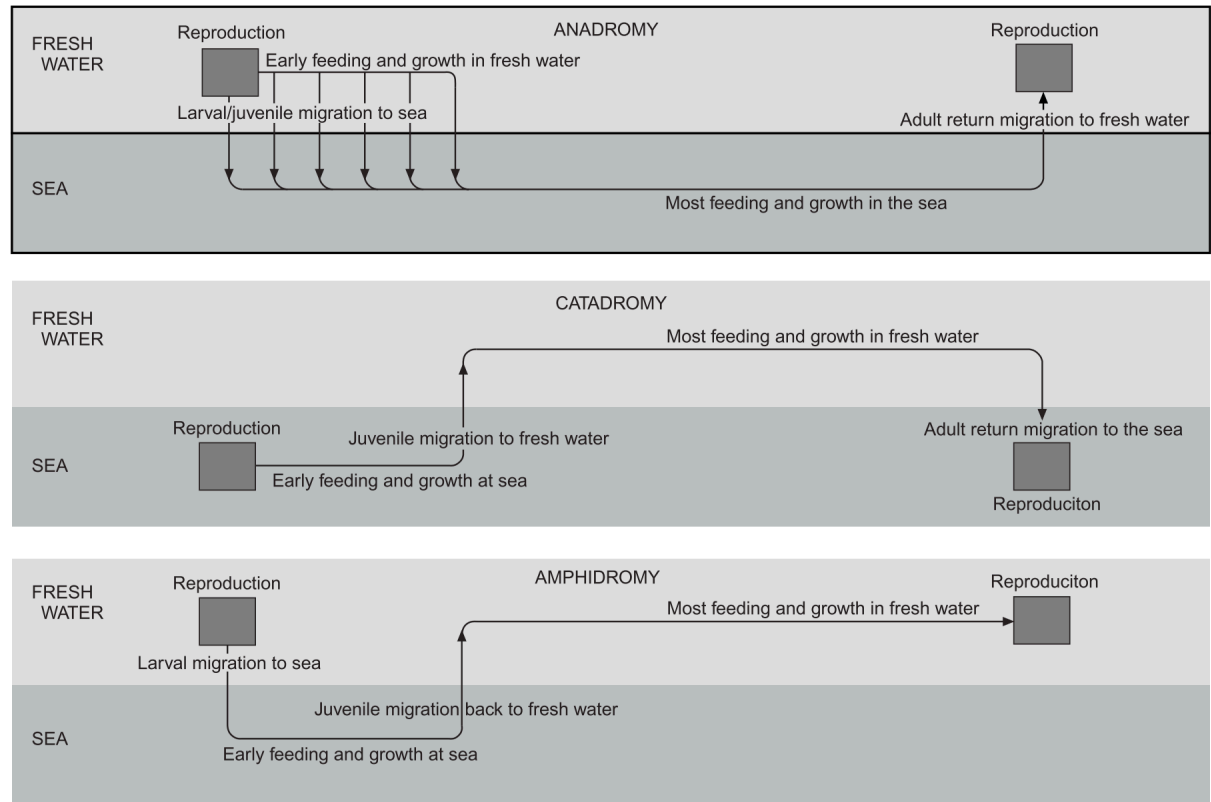
Figure 2. Map of sampled species and locations across Patagonia.
Estimated distribution range for native Chilean galaxiids (shaded and dash lined polygons) and the sampling locations of specimens used in this study (dots) for (A) genus Aplochiton, (B) genus Galaxias, (C) non-native fishes examined in this study. Made with Natural Earth. Free vector and raster map data at https://naturalearthdata.com.
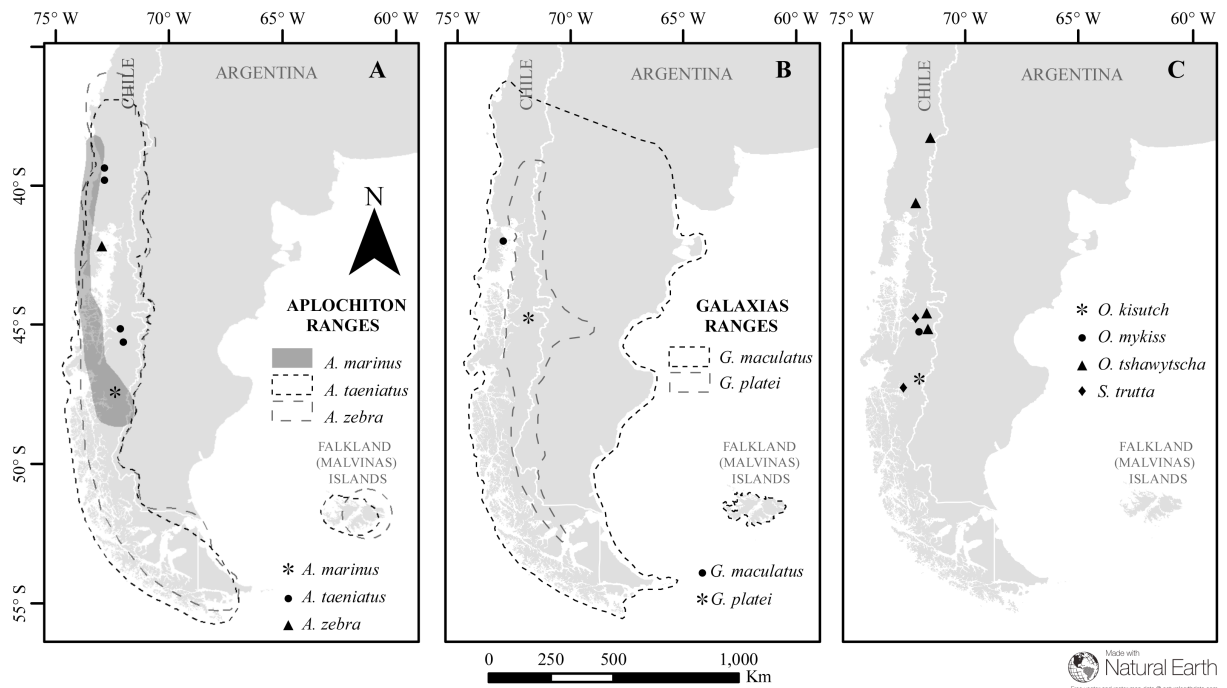
Figure 3. Idealized representations of resident and diadromous life-histories as expected in otolith microchemistry results.

The uppermost image depicts a schematic representation of an otolith, showing how growth rings accrue over time around the core and culminate at the edge. The number of distinct layers in the otolith depends on the age of the individual. The images below represent idealized time series data obtained by repeatedly measuring (via laser ablation and spectrometry) elemental strontium to calcium (Sr:Ca) ratios across the otolith. Each box shows an expected time series for each life-history strategy.

EDGE

CORE

TIME SERIES TRANSECT LINE

DIRECTION OF ACCUMULATION OF OTOLITH LAYERS

FRESHWATER

SALTWATER

BRACKISH

CATADROMY

ANADROMY

AMPHIDROMY

Transect Distance (µm)

Sr:Ca mmol·mol-1
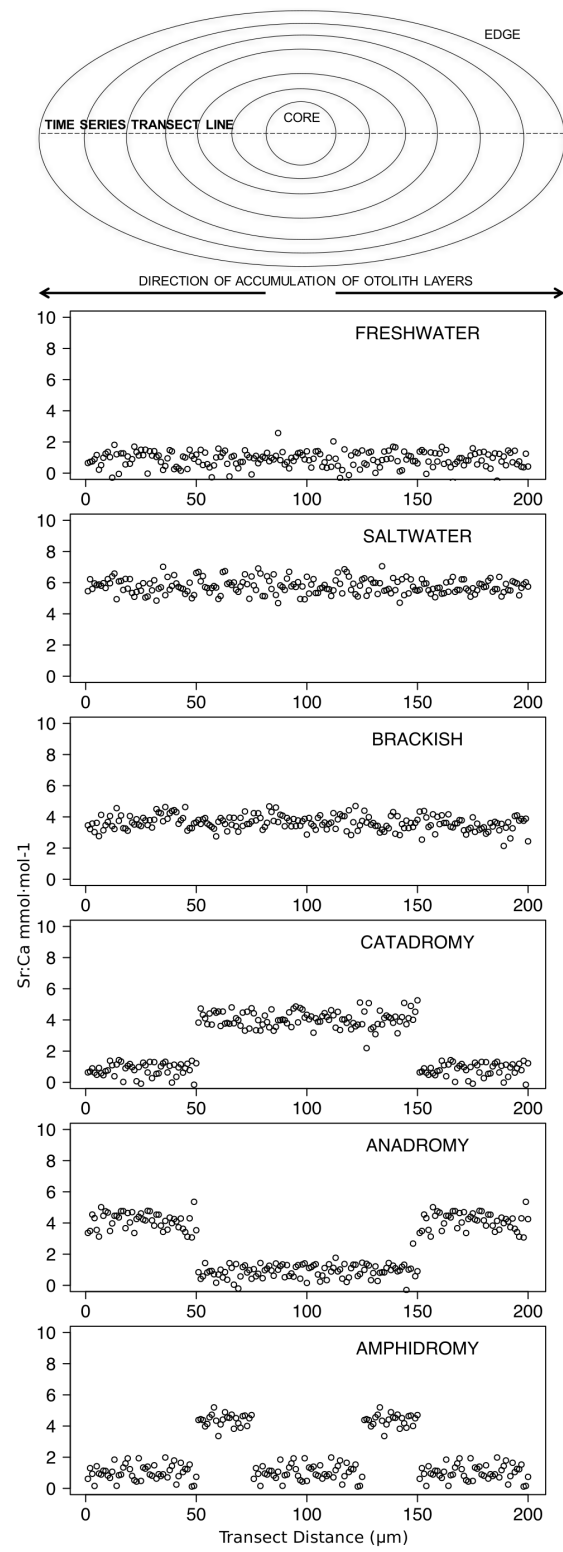
Figure 4. Violin plot for Sr:Ca values.
This plot reports the Sr:Ca values for otoliths grouped by species. Black dot, median; white line, first to third quartile. Grey areas, kernel density plot.
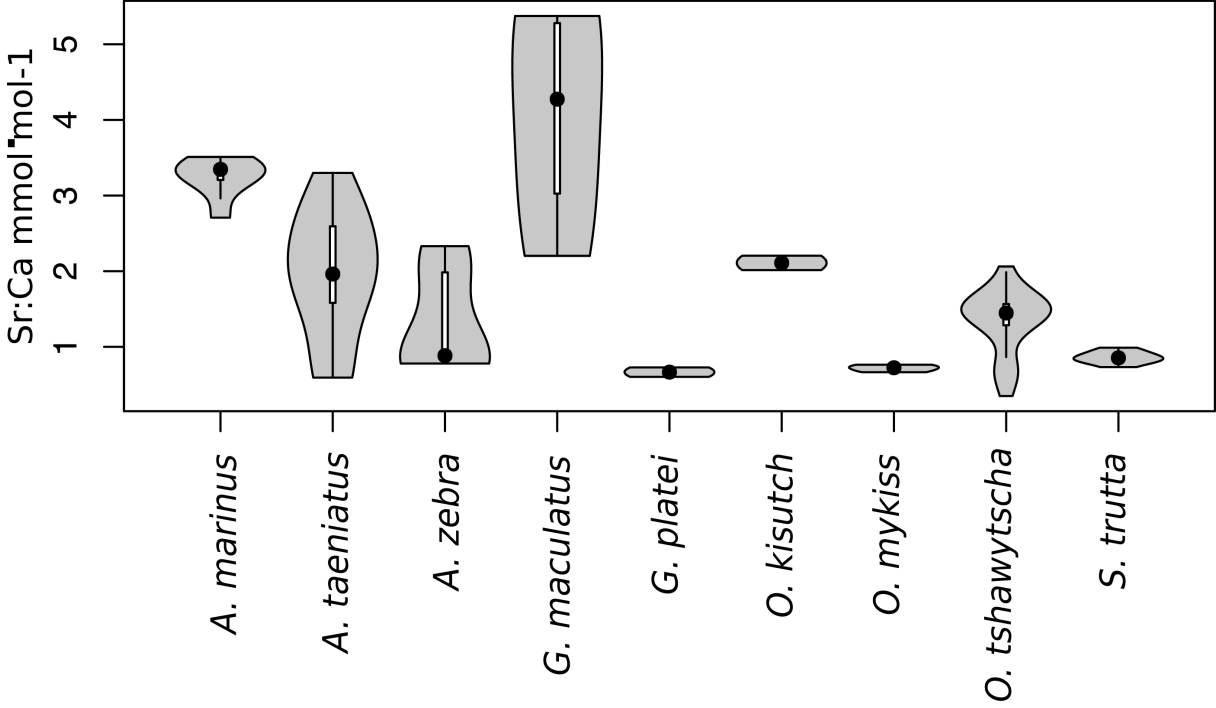
Figure 5. Detection of discontinuities by semi-supervised CART employed on Sr:Ca ratios for representative individuals of native and exotic fishes in southern Chile.
Numbers after taxonomic names refer to the individual ID of each fish. The mean for each cluster is represented by a continuous black line delimited by a grey box as standard deviation. Vertical dashed lines indicate splitting points induced by the condition used to fit the regression trees, which is reported for each individual graph as "cond".

A. zebra 3094
cond. = 0.5

O. tshawytscha 4338
cond. = 0.7

A. taeniatus 4359
cond. = 1.0

S. trutta 3426
cond. = 0.5

A. marinus 3697
cond. = 1.0

O. mykiss 3038
cond. = 0.5

G. platei 315
cond. = 0.5

O. kisutch 1153
cond. = 0.7

G. maculatus 4085
cond. = 1.0

O. tshawytscha 3747
cond. = 0.5

Sr:Ca mmol·mol-1

Relative Transect Distance (5μm)
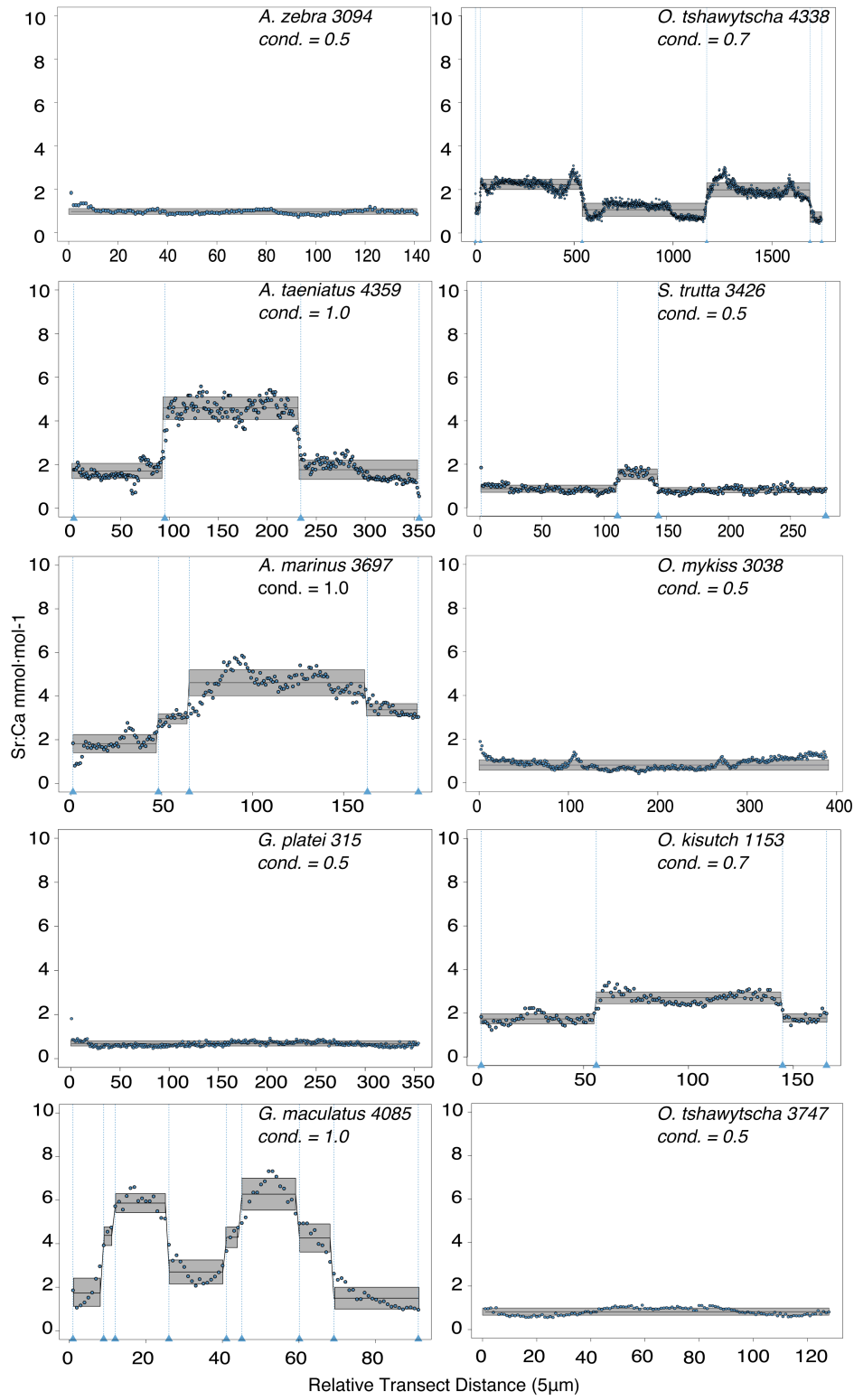
Figure 6. Total number of splits obtained by semisupervised CART on univariate Sr:Ca otolith data for all the species included in the study.

Frequency of the total number of splits obtained with different conditions (Cond) by semisupervised CART on univariate Sr:Ca otolith data for all the species included in the study. Original data for native *A. taeniatus*, *A. marinus*, and *G. maculatus* and introduced *O. tshawytscha* was divided in more than one homogenous cluster by semisupervised regression trees and led to rejection of the hypothesis of freshwater residency. "Trans" refers to the quality of the otolith transect, that is: "F" is a full or good quality transect, edge –core –edge, "H" is a half transect, edge –core; "P" is a partial transect, edge –core –extra data without reaching the next otolith edge; "O" is a flagged transect which failed to go through the core and may have some missing data. "St" refers to each fish's ontogenetic phase at the time of capture, where "J" is for juveniles and "A" for adult specimens; "Loc" indicates the sampling locality where AC: Aysén-Caro, CT: Chiloé-Tocoihue, VS: Valdivia-Santo Domingo, VL: Valdivia-Lingue, AP: Aysén-Palos, BE: Baker-estuary, AN: Aysén-Ñireguao, BJ: Baker-Jaramillo, PP: Petrohué-Patos, TP: Toltén-Peuco, TT: Toltén-Truful, AS: Aysén-Simpson, BV: Baker-Vargas; "Id" is the unique identification of each fish.
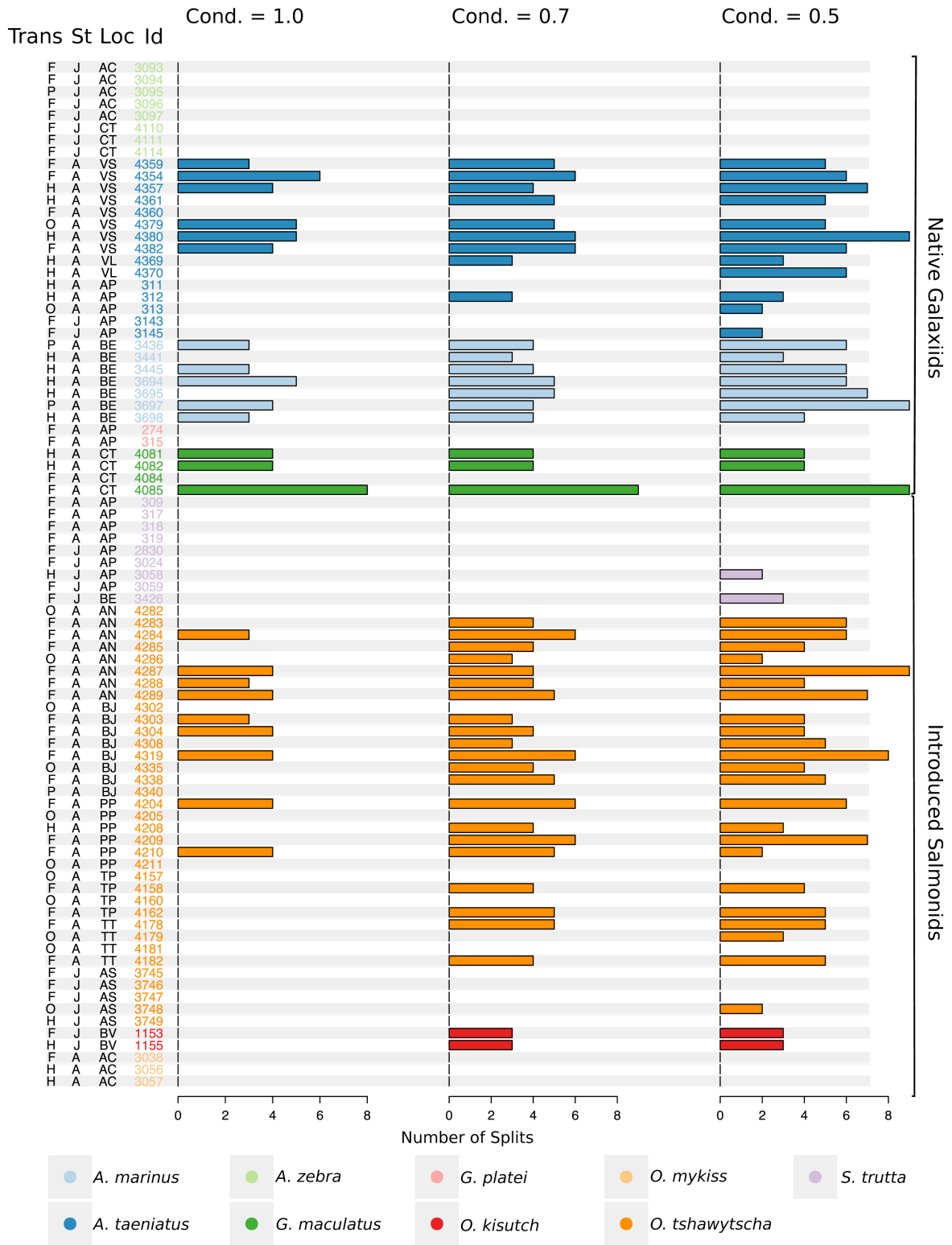
Figure 7. Global species diversity gradients for migratory species.
A: anadromous, B: catadromous, C: amphidromous, D: potamodromous, E: oceanodromous
Continent shapefile by ArcGIS, ESRI (www.arcgis.com). Geographic coordinate system WGS 1984 and projected to cylindrical equal area.
URL: https://www.arcgis.com/home/item.html?id=5cf4f223c4a642eb9aa7ae1216a04372
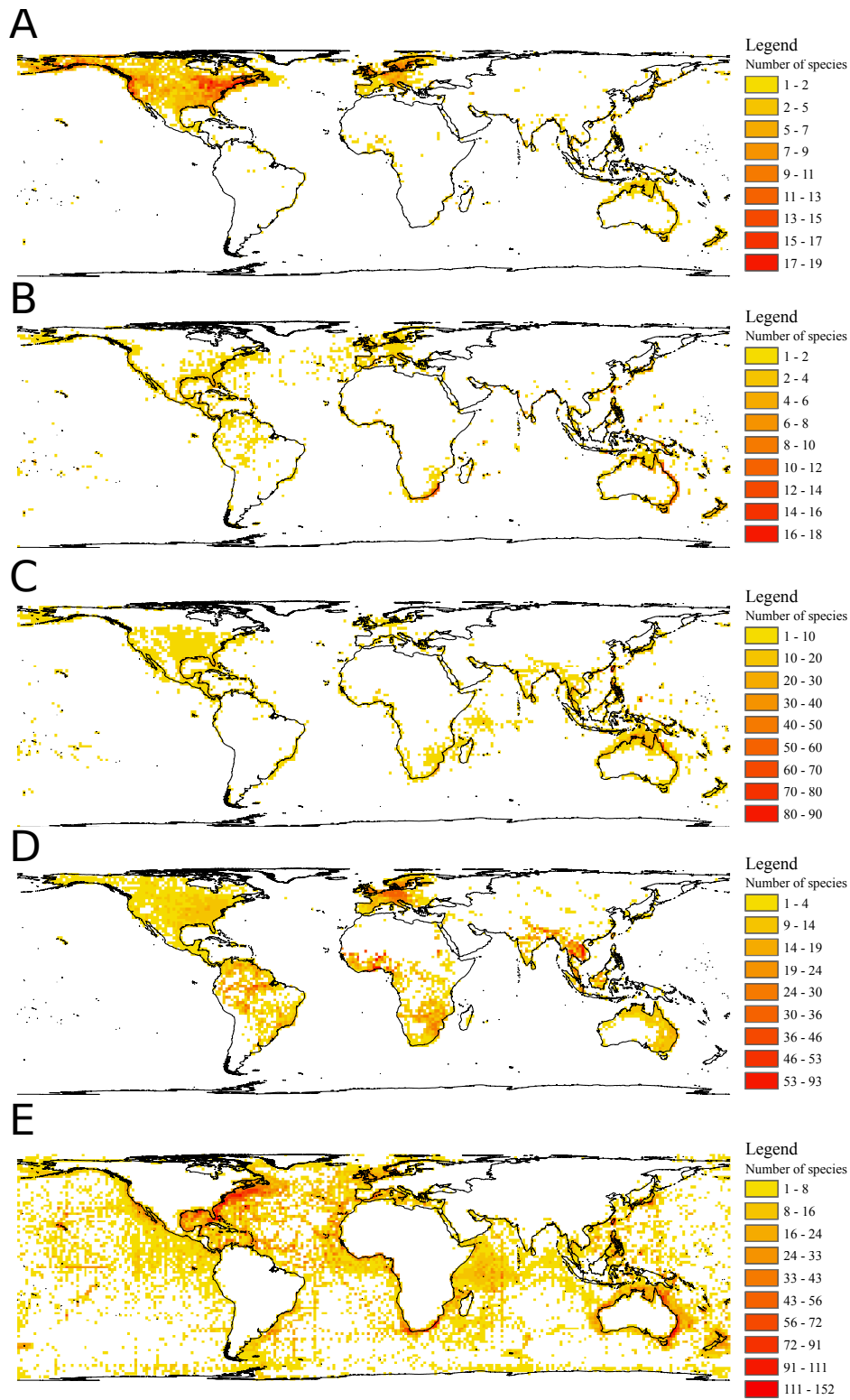
Figure 8. Species richness (SR) of each migratory group measured across segments of 10 degrees of latitude. Relative abundance of most relevant orders is shown in different colors. A: anadromous, B: catadromous, C: amphidromous, D: potamodromous, E: oceanodromous
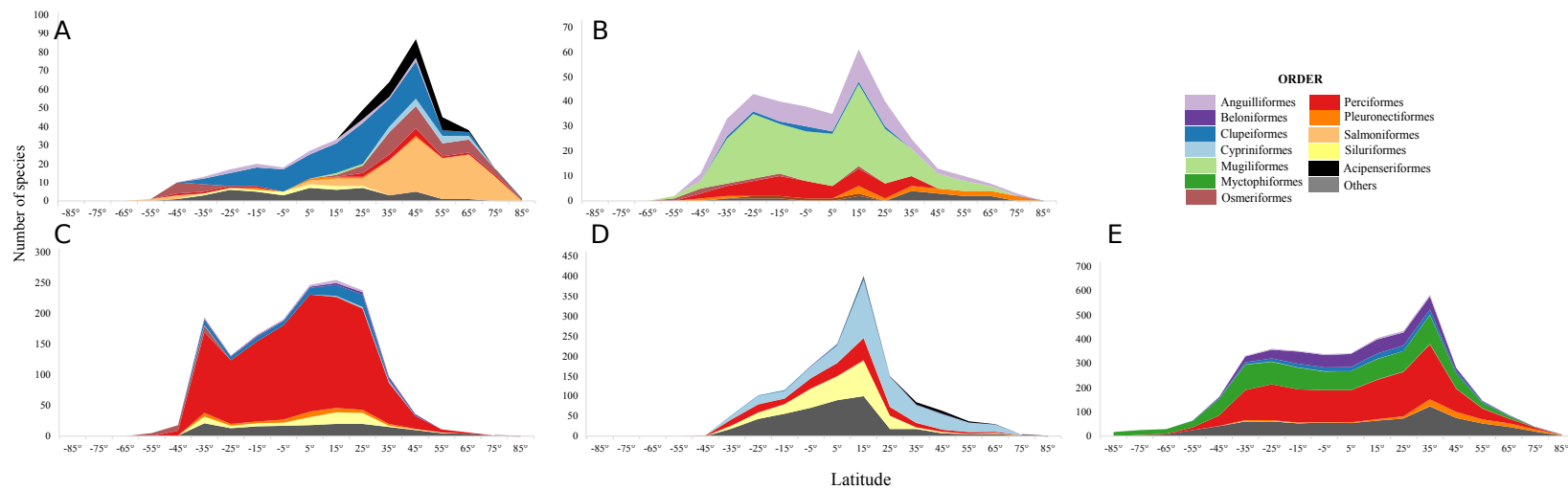
Figure 9. Temperature and biodiversity relationship for migratory and non-migratory species. Ana: anadromous, Cat: catadromous, Amp: amphidromous, Pot: potamodromous, Oce: oceanodromous, RES_FW: Freshwater residents, RES_OCE: Ocean residents, ALL: All species pooled together. Red dashed lines reflect data for each strategy as calculated in this study and blue dashed lines are the predicted trends according to Allen, Brown & Gillooly (2002).

ANA
y = 9.87 -2.01 x
r^2 = 0.1

CAT
y = 23.18 -5.86 x
r^2 = 0.77

AMP
y = 42.35 -11.1 x
r^2 = 0.95

POT
y = 26.48 -6.47 x
r^2 = 0.63

OCE
y = 26.82 -6.23 x
r^2 = 0.73

RES_FW
y = 38.4 -9.7 x
r^2 = 0.85

RES_OCE
y = 40.88 -10.34 x
r^2 = 0.86

ALL
y = 37.95 -9.11 x
r^2 = 0.83
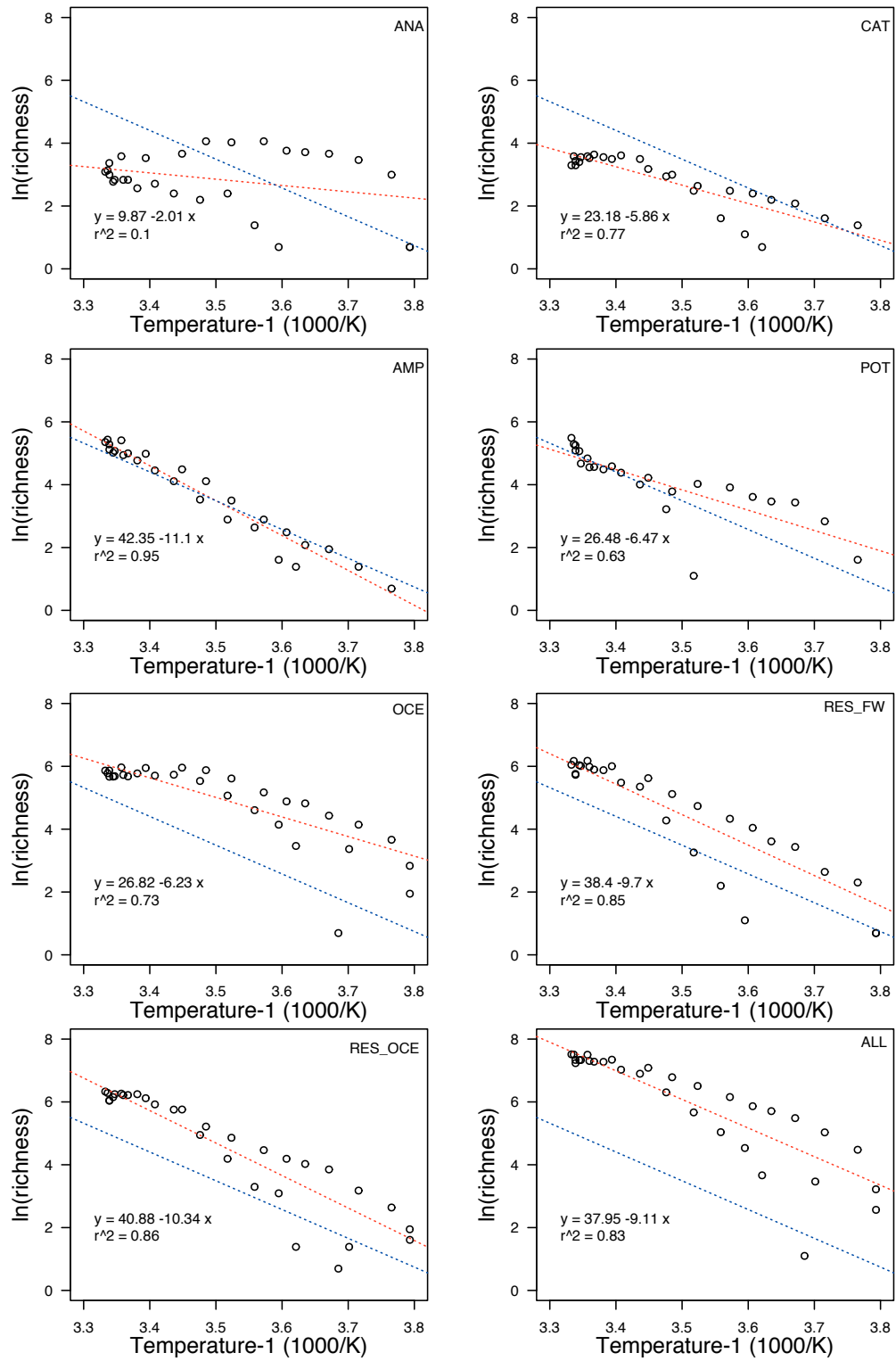
Figure 10. Causal diagram indicating the hypothesized relationship tested between latent variables for diadromous, potamodromous, and freshwater resident species.
The causal diagram for oceanodromous and ocean resident species involves the same latent variables (except precipitation) but different manifest variables were used to support some latent constructs (details of the manifest variables used are listed in Chapter 2, Methods section and in Table 5).
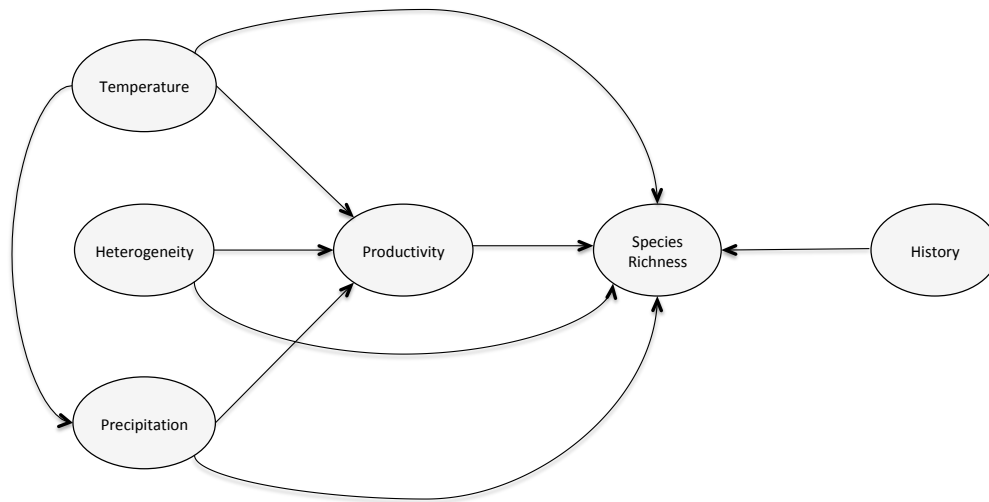
Figure 11. Barplot of path coefficients for migratory and resident strategies.
It represents the total effects of each latent variable as a function of direct and indirect effects
ana: anadromous, cat: catadromous, amp: amphidromous, pot: potamodromous, oce:
oceanodromous, oce_res: ocean residents, fw_res: freshwater residents.
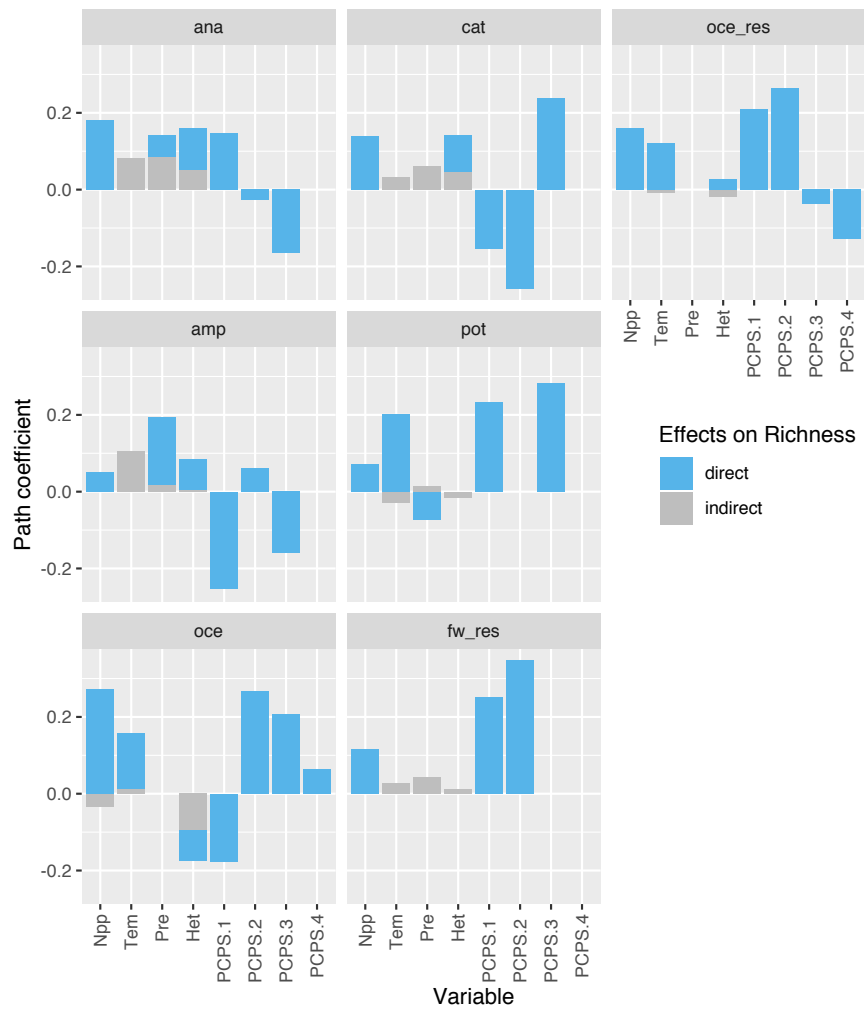
Figure 12. Redundancy analysis (RDA) plot.
Combines regression and PCA (Legendre and Legendre 1998; Borcard et al. 2009) to model selected environmental, productivity and PCPS phylogenetic filters. PCPSs are vectors of genetic structure based on phylogenetic distance data (Pillar and Duarte 2010) calculated from a backbone phylogenetic tree (Rabosky et al. 2018).
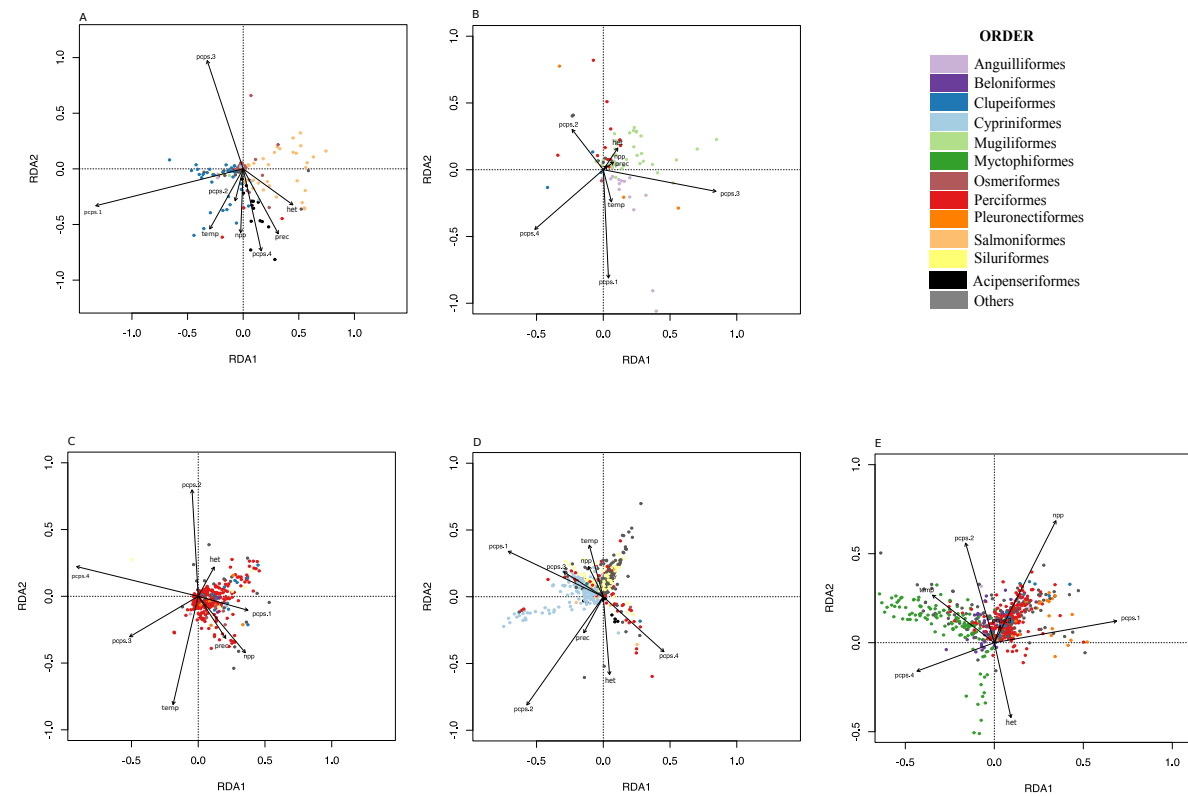
Figure 13. Mean speciation rates of Actinopterygian fishes subdivided by movement strategy.
The speciation rate dynamics were inferred with Bayesian analysis of macroevolutionary mixtures (BAMM) (Rabosky et al., 2018) and subdivided by their life-history strategies according to information collected on Fishbase (Froese & Pauly, 2016).
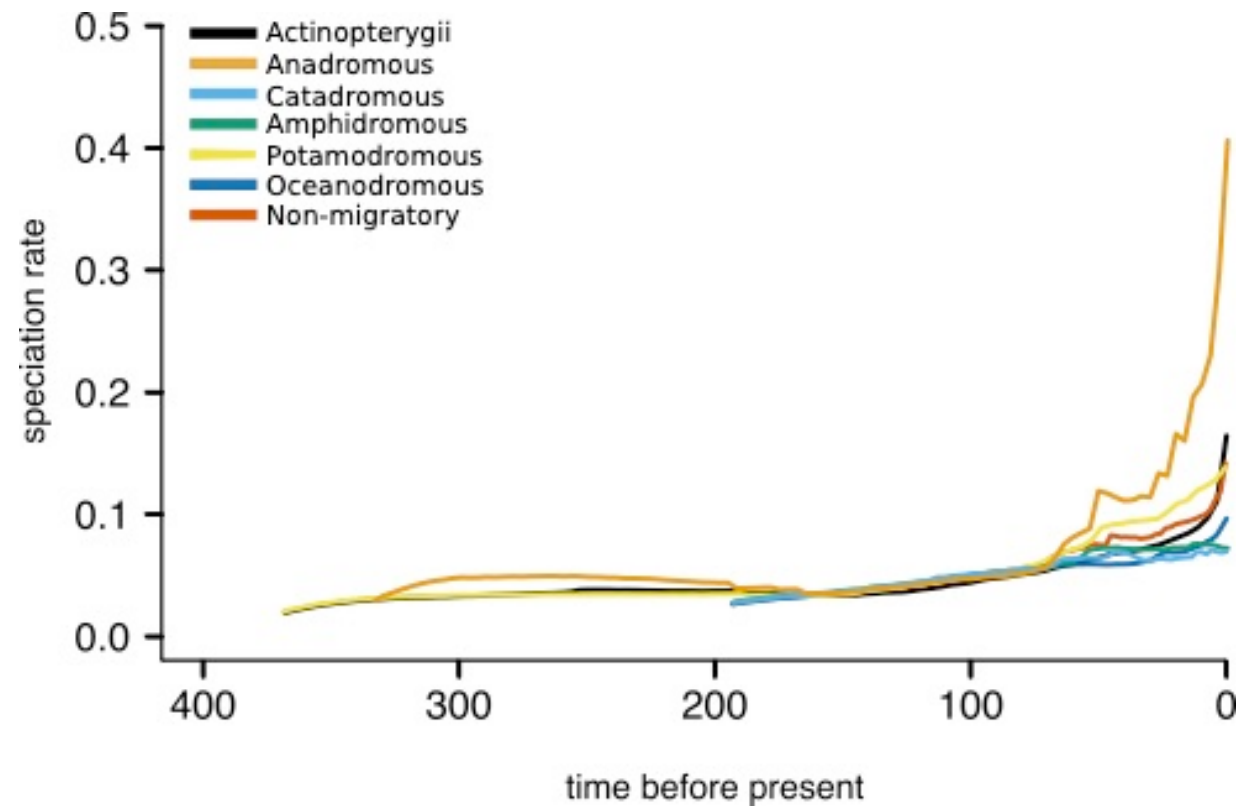
Figure 14. Time tree map adapted from (Rabosky et al. 2018).

Lambda values are shown in colors on the branches of the tree according to the heat scale (note the different scale in each graph). Horizontal bars "Mig" in the first graph (migratory) represent migrants according to their category. Latitudinal horizontal bars are drawn in respect to the species' known minimum and maximum latitudes. The families listed are for referencing phylogenetic areas with higher speciation rates. Panel "A" shows migratory fishes, panel "B" brackish and panel "C" freshwater.

A.
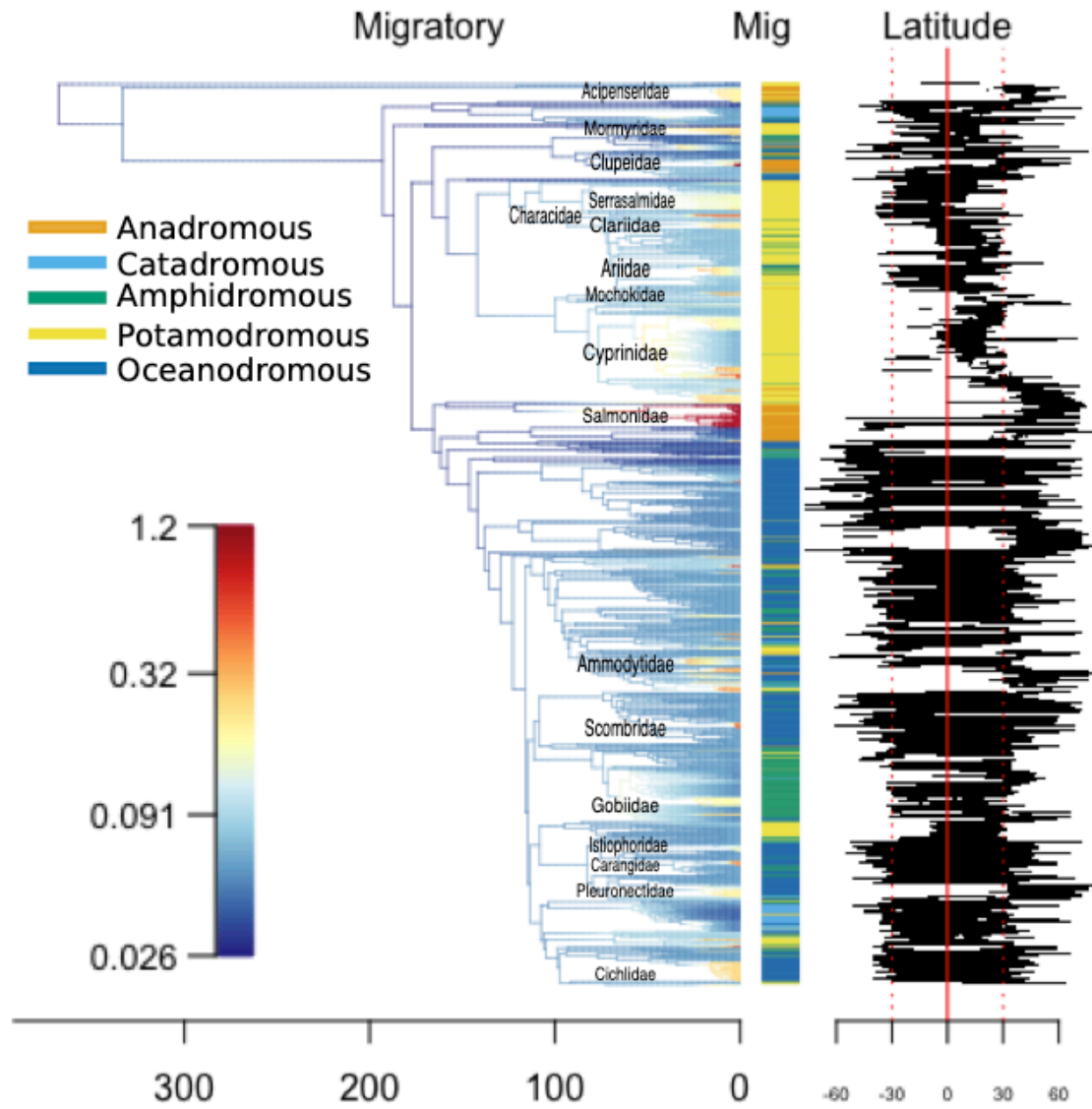
B.
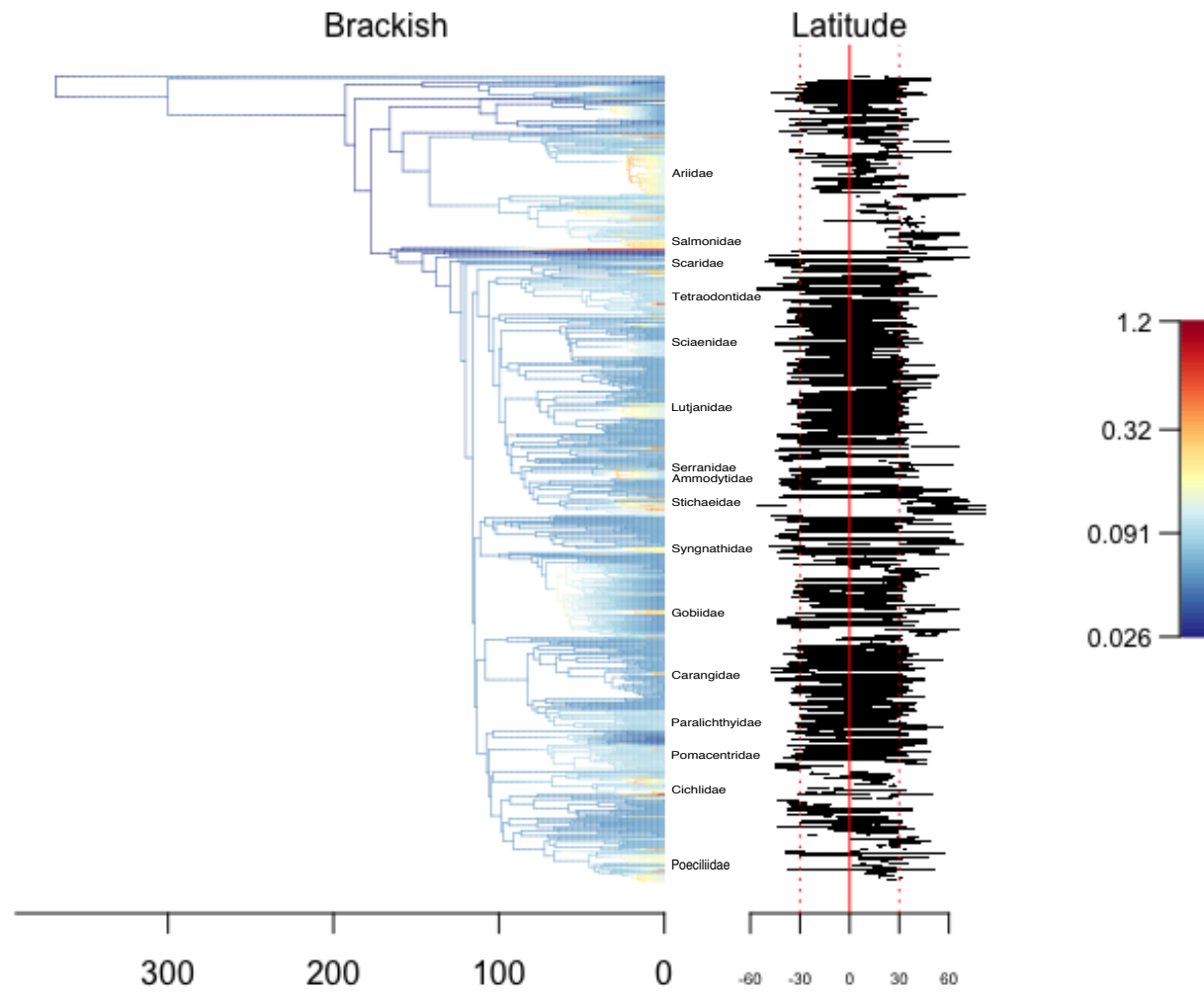
C.
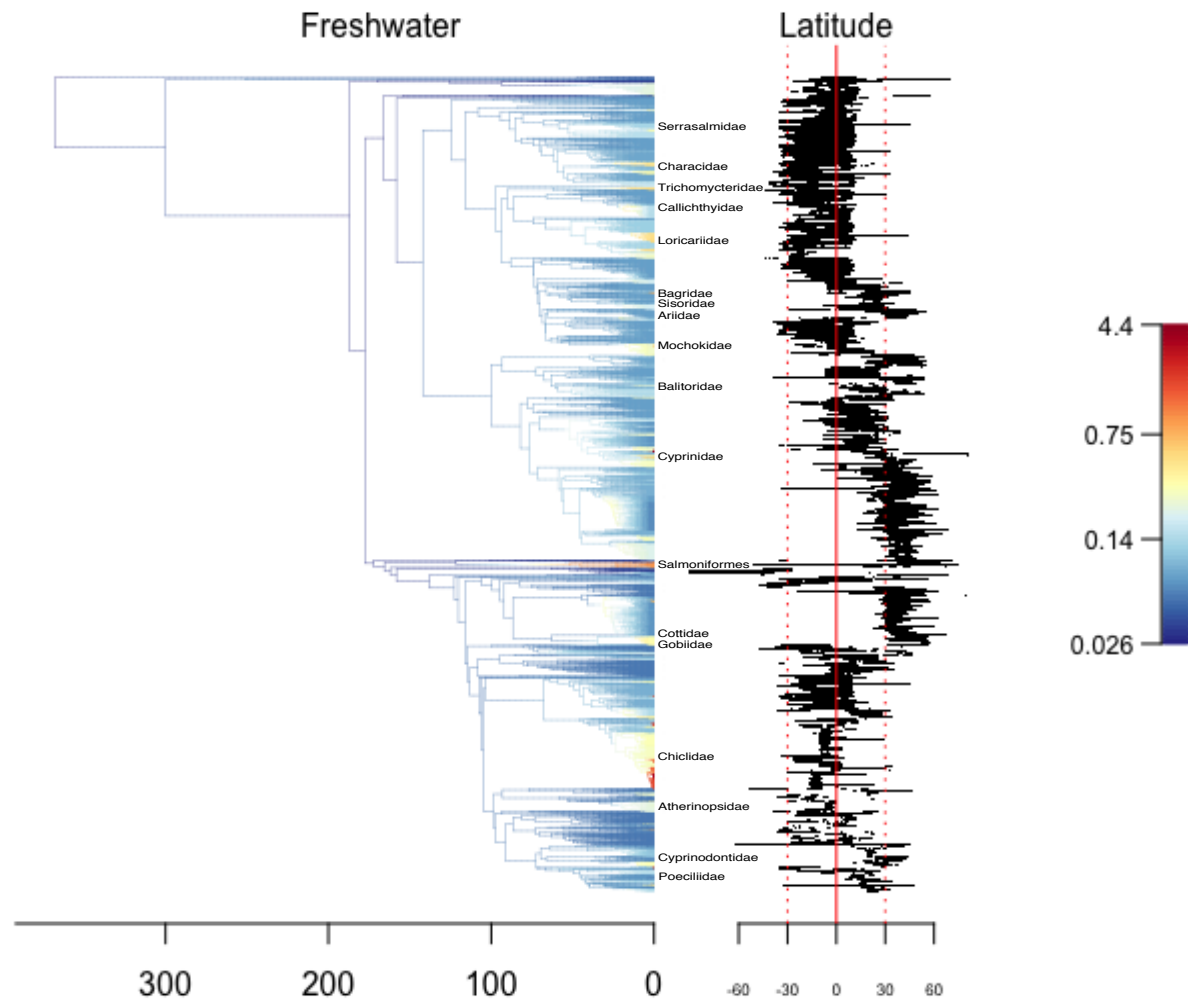
Figure 15. Midpoint latitude and speciation rate of resident and migratory fishes.
The relationship between midpoint latitude and the speciation rate for each species included in this study, separated by their movement life-history strategy, residents in panel A, and migratory fishes in panel B.
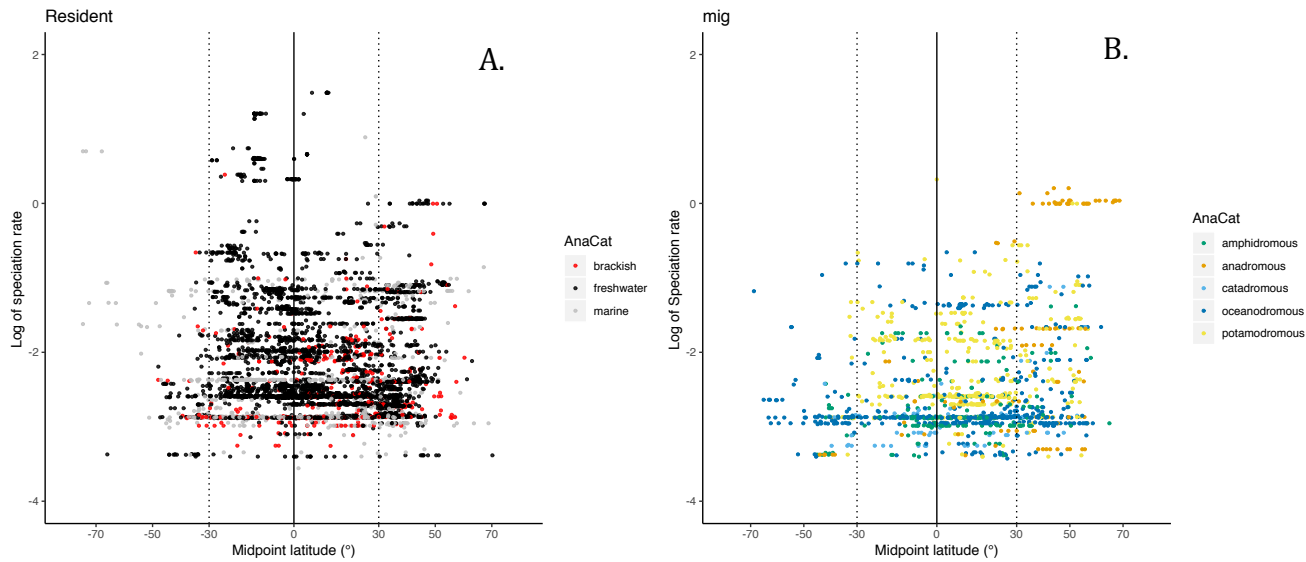
Figure 16. Correlations of latitude with speciation rate across life-history strategies.
Spearman's correlation values of the relationship between absolute values of latitude and the logarithmic transformed speciation rate for each migratory and resident strategy.
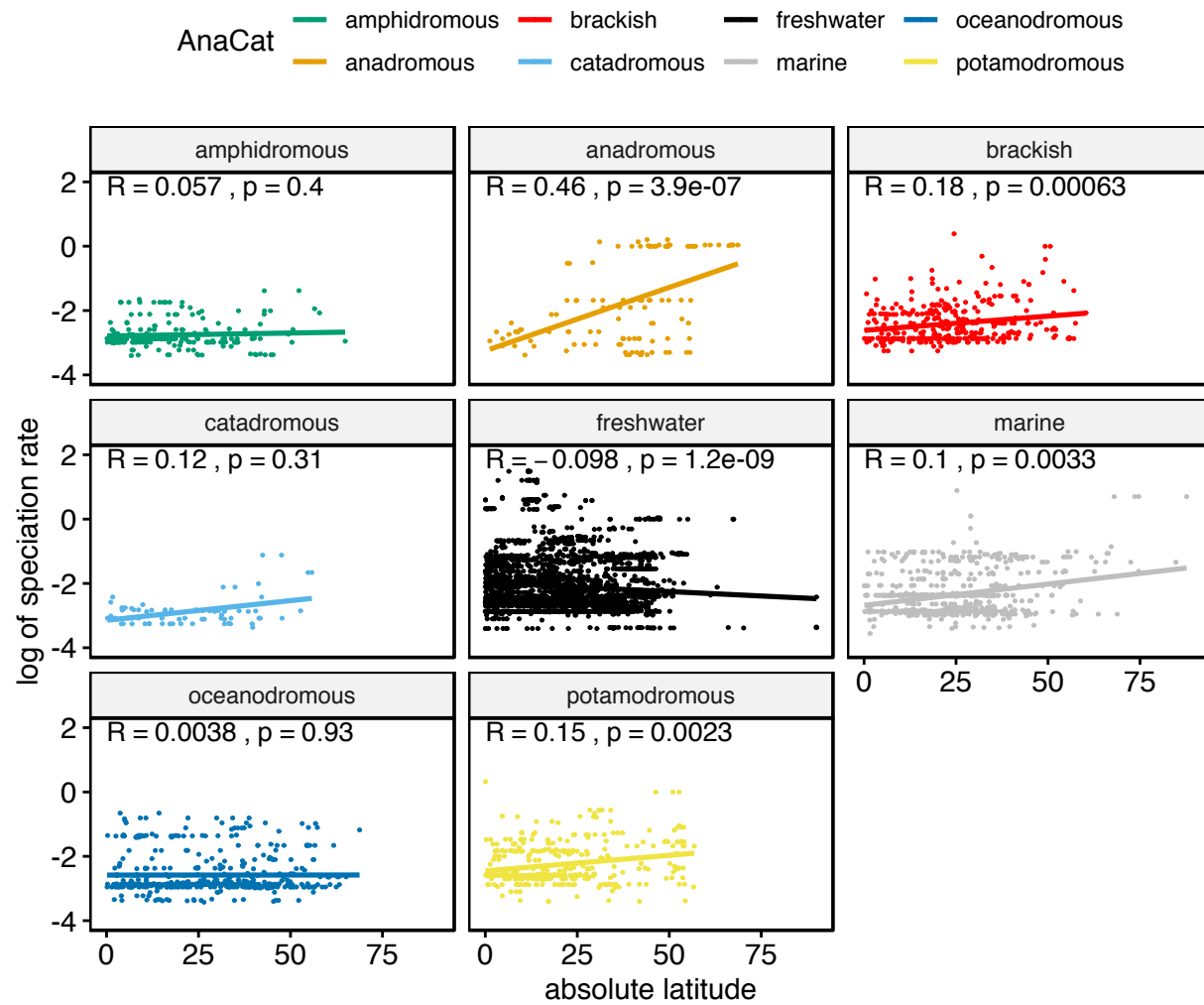
Figure 17. Frequency of migrants and speciation rate.
Each fish clade is plotted against the frequency of migrants in each. Panel A is the frequency of migrants in each family, colored according to the Order to which each group belongs. Panel B is the frequency of migrants in all orders of Actinopterygian fishes. Species richness is represented by the size of each point and was calculated as the number of species in each family and order. The dashed line represents the linear model regression between the speciation rate and the frequency of migrants.
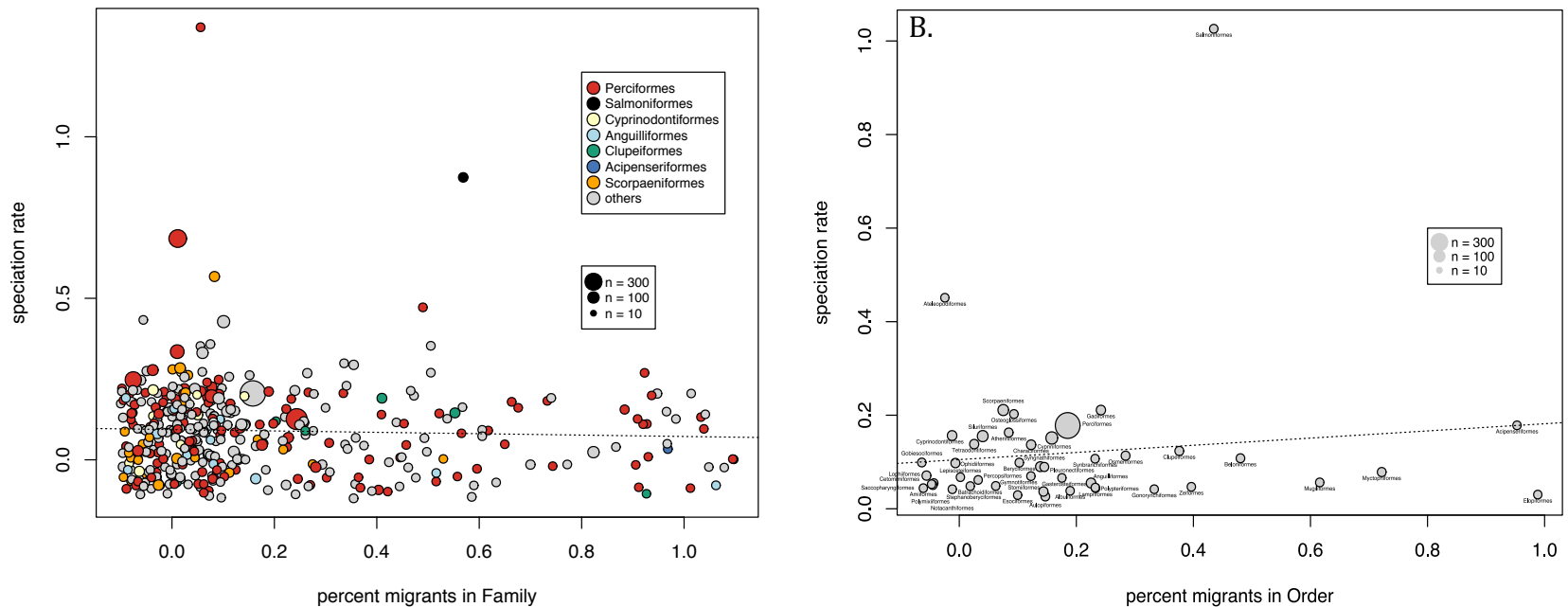
SUPPLEMENTAL INFORMATION

SUPPLEMENTAL TABLES

Table S1. Native continental fishes of Chile and their life-history.
The following table lists the native continental fishes of Chile, highlighting current knowledge about their preferred habitat and/or life history. Abbreviations in the Life history/habitat column correspond to: A, anadromous; C, catadromous; Am, amphidromous; P, potadromous; FW, obligate freshwater resident; E, euryhaline; SW, indicates either estuarine preference or pseudo complete ocean residency.

FAMILY	GENUS	SPECIES	LIFE HISTORY/HABITAT	GEOGRAPHIC RANGE (Origin)	REFERENCES
Petromyzontidae	*Geotria*	*australis (Gray, 1851)*	A	Southern Hemisphere	(McDowall 1988; Neira et al. 1988)
Petromyzontidae	*Mordacia*	*lapicida (Gray, 1851)*	A	Chile	(McDowall 2002a)
Characidae	*Cheirodon*	*pisciculus (Girard, 1855)*	FW	Chile	(Salas et al. 2012)
Characidae	*Cheirodon*	*australe (Eigenmann, 1927)*	FW	Chile	(Salas et al. 2012)
Characidae	*Cheirodon*	*galusdae (Eigenmann, 1928)*	FW	Chile	(Salas et al. 2012)
Characidae	*Cheirodon*	*kiliani (Campos, 1982)*	FW	Chile	(Salas et al. 2012)
Diplomystidae	*Diplomystes*	*chilensis (Molina, 1782)*	FW	Chile	(Munoz-Ramirez et al. 2010)
Diplomystidae	*Diplomystes*	*camposensis (Arratia, 1987)*	FW	Chile	(Munoz-Ramirez et al. 2010)
Diplomystidae	*Diplomystes*	*nahuelbutaensis (Arratia, 1987)*	FW	Chile	(Munoz-Ramirez et al. 2010)
Trichomycteridae	*Nematogenys*	*inermis (Guichenot, 1848)*	FW	Chile	(Habit and Victoriano 2005; Vargas et al. 2015)
Trichomycteridae	*Trichomycterus*	*areolatus (Valenciennes, 1846)*	FW	Chile	(Unmack et al. 2009)
Trichomycteridae	*Trichomycterus*	*chiltoni (Eigenmann, 1928)*	FW	Chile	(Habit and Victoriano 2005)

Trichomycterida e	*Trichomycterus*	*rivulatus (Valenciennes, 1846)*	FW	Chile, Peru, Bolivia	(Pardo et al. 2005; Habit et al. 2006)
Trichomycterida e	*Trichomycterus*	*chungaraensis (Arratia 1983)*	FW	Chile	(Arratia F. 1983; Vargas et al. 2015)
Trichomycterida e	*Trichomycterus*	*laucaensis (Arratia 1983)*	FW	Chile	(Arratia F. 1983; Vargas et al. 2015)
Trichomycterida e	*Hatcheria*	*macraei (Berg, 1985)*	FW	Chile, Argentina	(Unmack et al. 2012; Vargas et al. 2015)
Trichomycterida e	*Bullockia*	*maldonadoi (Eigenmann, 1920)*	FW	Chile	(Habit and Victoriano 2005)
Galaxiidae	*Galaxias*	*maculatus (Jenyns, 1842)*	C	Southern Hemisphere	(Górski et al. 2015; Vargas et al. 2015)
Galaxiidae	*Galaxias*	*globiceps (Eigenmann, 1928)*	FW	Chile	(Murillo & Ruiz 2002)
Galaxiidae	*Galaxias*	*platei (Steindachner, 1898)*	FW	Chile, Argentina	(Ruzzante et al. 2008; Vargas et al. 2015)
Galaxiidae	*Brachygalaxias*	*bullocki (Regan, 1908)*	FW	Chile	(Habit and Victoriano 2005; Correa-Araneda et al. 2014; Vargas et al. 2015)
Galaxiidae	*Brachygalaxias*	*gothei (Busse, 1983)*	FW	Chile	(Cuevas et al. 1999; Vargas et al. 2015)
Galaxiidae	*Aplochiton*	*zebra (Jenyns, 1842)*	FW	Chile, Argentina, Malvinas	(Vargas et al. 2015)
Galaxiidae	*Aplochiton*	*taeniatus (Jenyns, 1842)*	C	Chile, Argentina, Malvinas	(Vanhaecke et al. 2012; Alò et al. 2013; Vargas et al. 2015)
Galaxiidae	*Aplochiton*	*marinus (Eigenmann, 1928)*	C	Chile	(Alò et al. 2013; Vargas et al. 2015)
Atherinopsidae	*Basilichthys*	*microlepidotus (Jenyns, 1841)*(syn:*australi s*)	FW	Chile	(Dyer 2000)
Atherinopsidae	*Basilichthys*	*semotilus (Cope, 1874)*	P	Chile, Peru	(Dyer 2000; Vargas et al. 2015)
Atherinopsidae	*Odontesthes*	*mauleanum (Steindachner, 1896)*	E	Chile	(Dyer 2000)

Atherinopsidae	*Odontesthes*	*itatanum (Steindachner, 1896)*	E	Chile	(Dyer 2000)
Atherinopsidae	*Odontesthes*	*brevianalis (Gunther, 1880)*	E	Argentina, Chile	(Dyer 2000; Ministerio del Medio Ambiente 2013)
Atherinopsidae	*Odontesthes*	*hatchery* (Eigenmann, 1909)	E	Argentina, Chile	(Tsuzuki et al. 2008; Ministerio del Medio Ambiente 2013)
Atherinopsidae	*Odontesthes*	*molinae (Fowler, 1940) or (Fischer, 1962)*	No information (Possible synonym with other Odontesthes)	Chile	(Campos et al. 1998; Vargas et al. 2015)
Atherinopsidae	*Odontesthes*	*regia* (Humboldt, 1821)	SW (Juveniles in estuarine)	Peru, Chile, Argentina, Malvinas	(Ministerio del Medio Ambiente 2013)
Atherinopsidae	*Odontesthes*	*nigricans* (Richardson, 1848)	SW (Juveniles in estuarine)	Chile, Argentina, Malvinas	(Dyer 2000)
Atherinopsidae	*Odontesthes*	*wiebrichi* (Eigenmann, 1928)	E (Possible hybrid regia/brevianalis)	Chile	(Dyer 2000)
Cyprinodontidae	*Orestias*	*agassii (Valenciennes, 1846)*	FW	Peru, Chile	(Diario Oficial de la Republica de Chile 2008; Vargas et al. 2015)
Cyprinodontidae	*Orestias*	*chungarensis (Arratia, 1982)*	FW	Chile	(Diario Oficial de la Republica de Chile 2008; Vargas et al. 2015)
Cyprinodontidae	*Orestias*	*parinacotensis (Arratia, 1982)*	FW	Chile	(Diario Oficial de la Republica de Chile 2008; Ministerio del Medio Ambiente 2013; Vargas et al. 2015)
Cyprinodontidae	*Orestias*	*laucaensis (Arratia, 1982)*	FW	Chile	(Diario Oficial de la Republica de Chile 2008; Ministerio del Medio Ambiente 2013)

| Family	Genus	Species	Habitat	Distribution	References
Cyprinodontidae	*Orestias*	*ascotanensis (Parenti, 1984)*	FW	Chile	(Pardo et al. 2005; Vila et al. 2007; Diario Oficial de la Republica de Chile 2008; Ministerio del Medio Ambiente 2013)
Cyprinodontidae	*Orestias*	*gloriae (Vila et al, 2011)*	FW (Saltpans)	Chile	(Vila et al. 2011)
Cyprinodontidae	*Orestias*	*piacotensis (Vila, 2006)*	FW	Chile	(Vila 2006; Ministerio del Medio Ambiente 2013)
Mugilidae	*Mugil*	*cephalus (Linnaeus, 1758)*	E/50km upstream FW	Worldwide coastal areas	(Habit and Victoriano 2005; Diario Oficial de la Republica de Chile 2008; Ministerio del Medio Ambiente 2013; Vargas et al. 2015)
Percichthyidae	*Percichthys*	*melanops (Girard, 1855)*	FW	Chile	(Habit and Victoriano 2005; Diario Oficial de la Republica de Chile 2008; Ministerio del Medio Ambiente 2013; Vargas et al. 2015)
Percichthyidae	*Percichthys*	*trucha (Regan, 1905)*	FW	Argentina, Chile	(Ruzzante et al. 2006; Diario Oficial de la Republica de Chile 2008; Vargas et al. 2015)
Perciliidae	*Percilia*	*gillissi (Girard, 1855)*	FW	Chile	(Habit and Victoriano 2005; Ministerio del Medio Ambiente 2013; Vargas et al. 2015)

Perciliidae	*Percilia*	*irwini (Eigenmann, 1928)*	FW	Chile	(Habit and Victoriano 2005; Diario Oficial de la Republica de Chile 2008; Min. del Medio Ambiente 2013)

**Table S2.** Unidimensionality values for latent variables**.**

C. alpha is the Cronbach's alpha, DG.rho is the Dillon-Goldstein's rho and eig.1st and eig.2nd are the first and second eigenvalues based on the eigen-analysis of the correlation matrix of each set of indicators (Sanchez 2013). Only values based on latent variables constructed by multiple manifest variables are shown

|	C.alpha	DG.rho	eig.1st	eig.2nd
Freshwater				
Temperature	0.953744515	0.963138732	4.881099889	0.865217052
Heterogeneity	0.975388639	0.987843908	1.951959617	0.048040383
Precipitation	0.978224282	0.983954777	3.755089847	0.149084731
Ocean				
Heterogeneity	0.881079952	0.943877048	1.787437809	0.212562191

SUPPLEMENTAL FIGURES

Figure S1. Path diagrams, coefficients and Goodness of Fit (GOF) measures for each strategy.
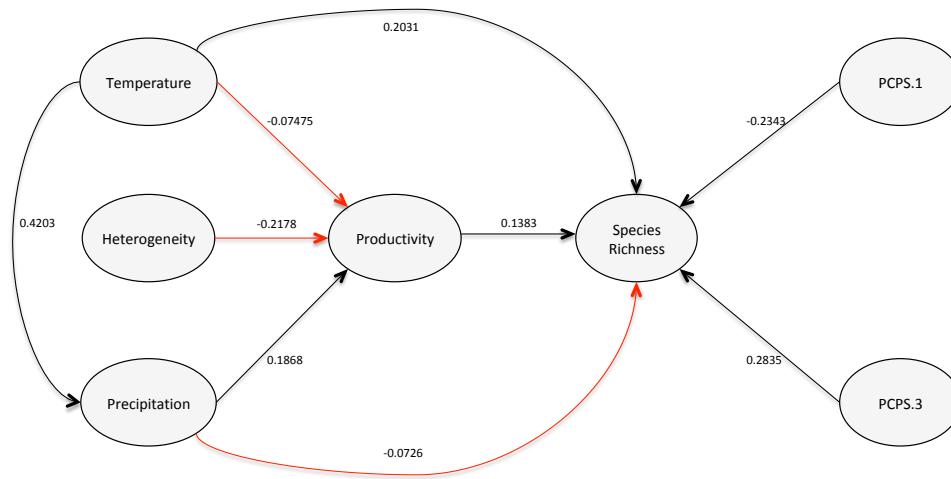

Anadromous
GoF = 0.4489
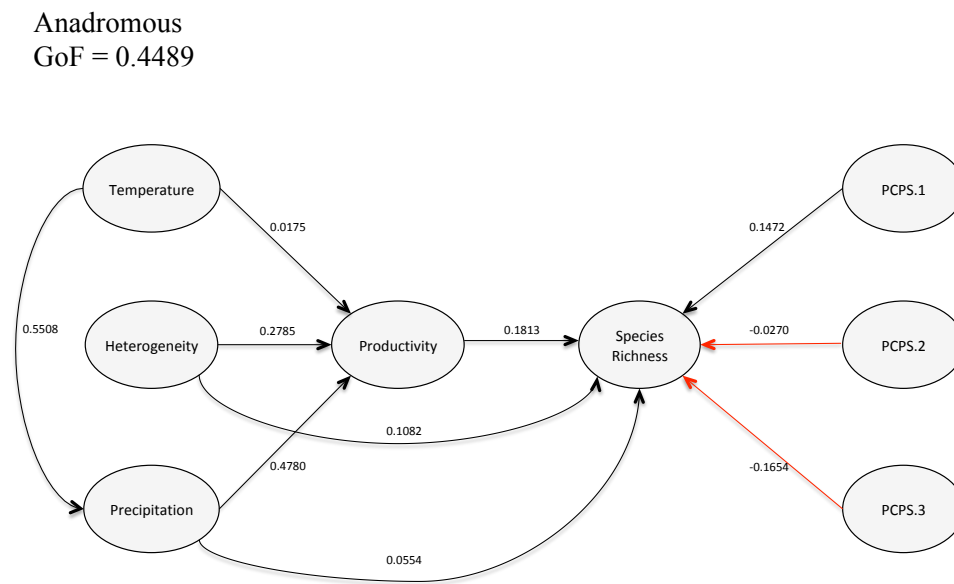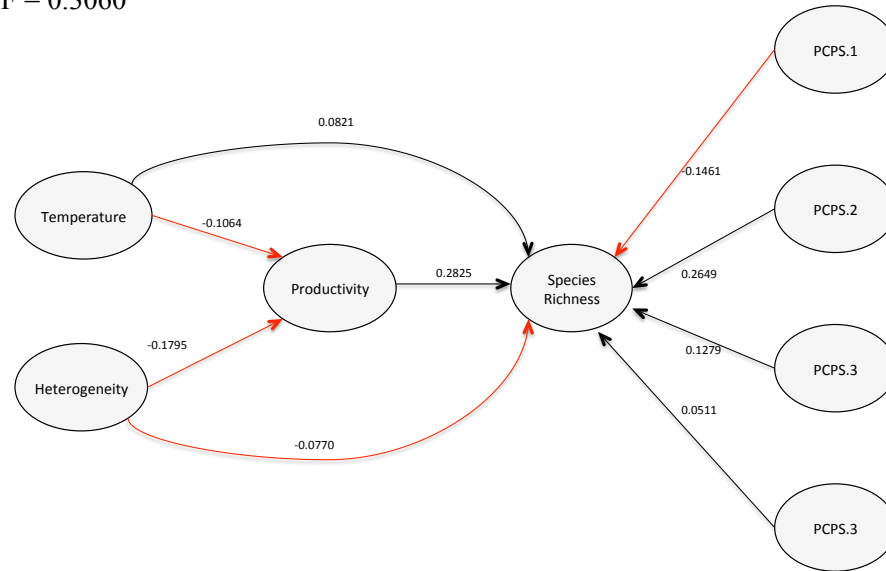
Catadromous
GoF = 0.4766
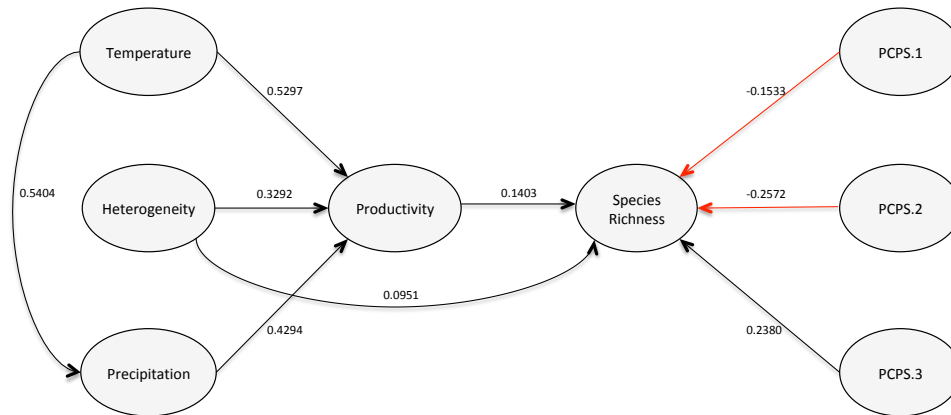
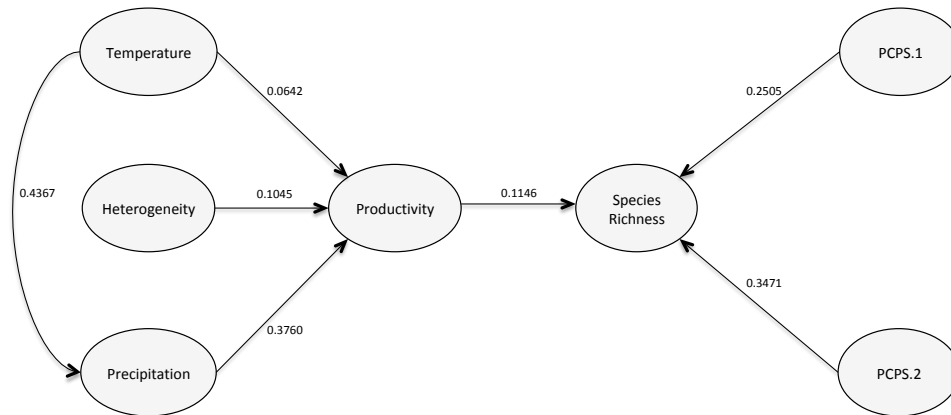Amphidromous
GoF = 0.4133
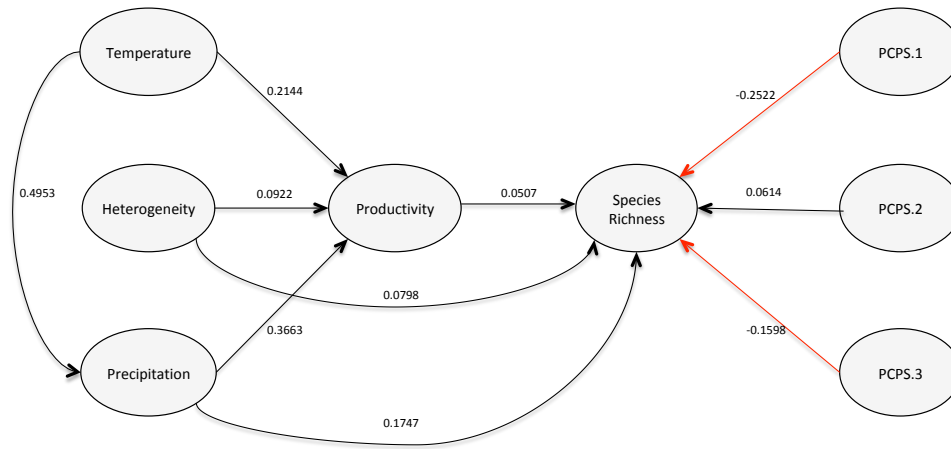
Potamodromous
GoF = 0.3474

Oceanodromous
GoF = 0.3060

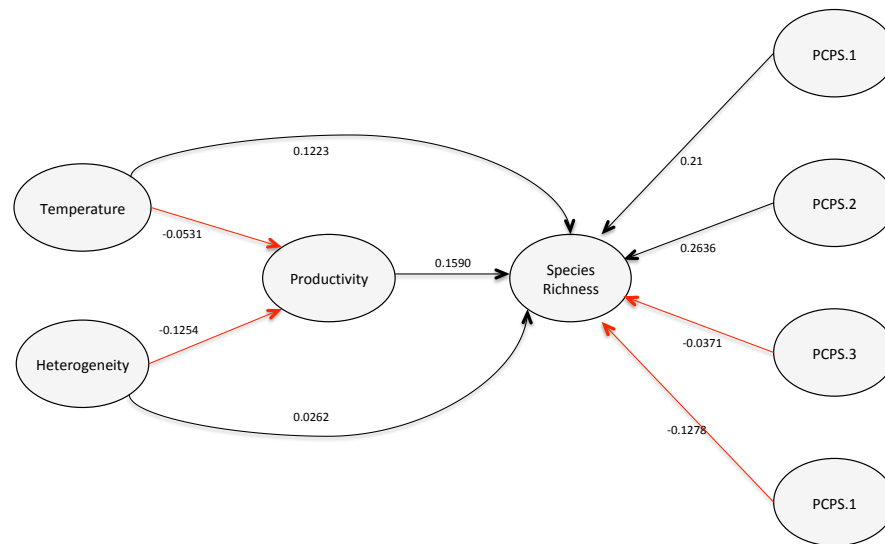Freshwater residents
GoF = 0.48

Ocean residents
GoF = 0.3335

Figure S2. Dot chart of Order, speciation rate and life-history strategies
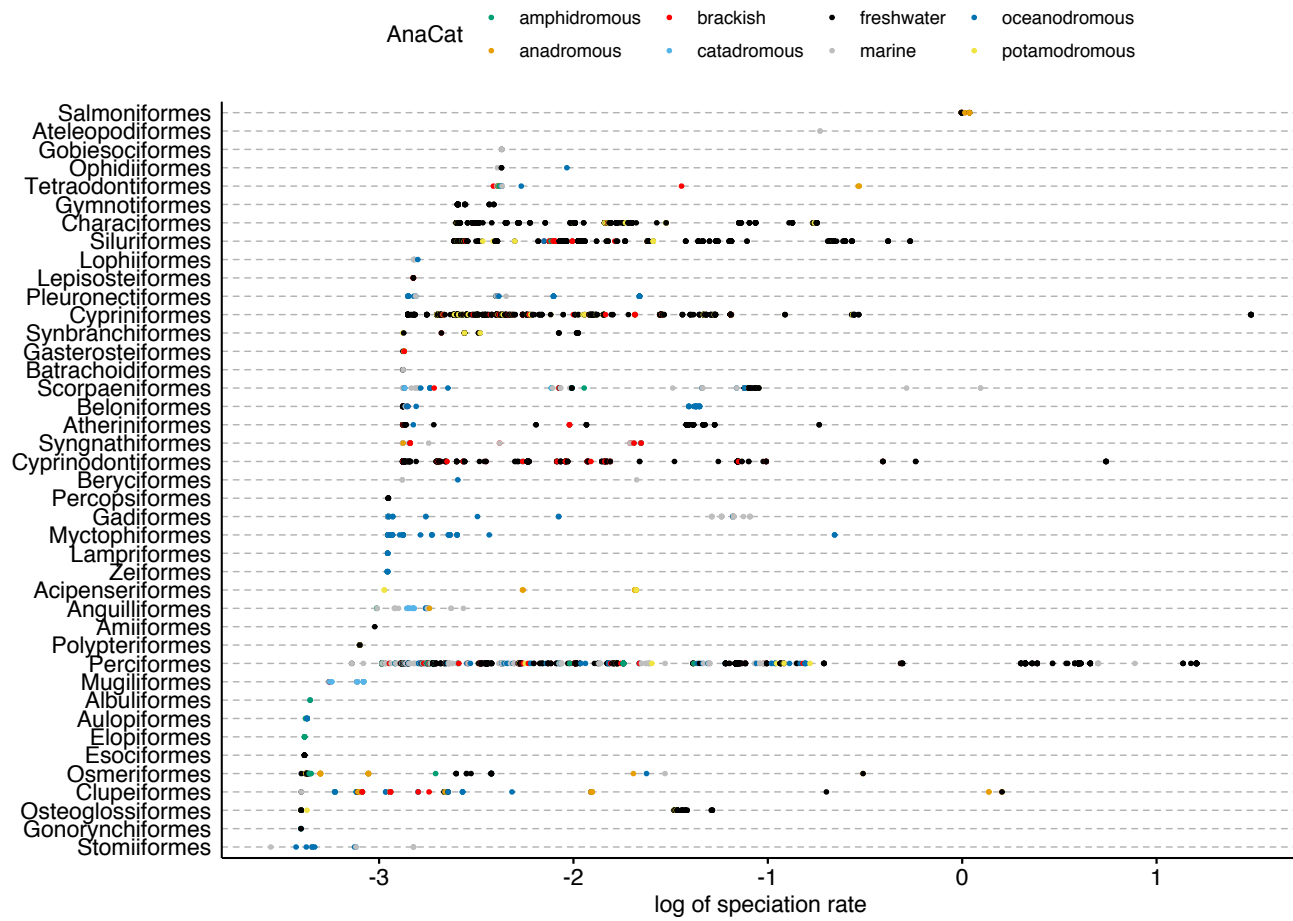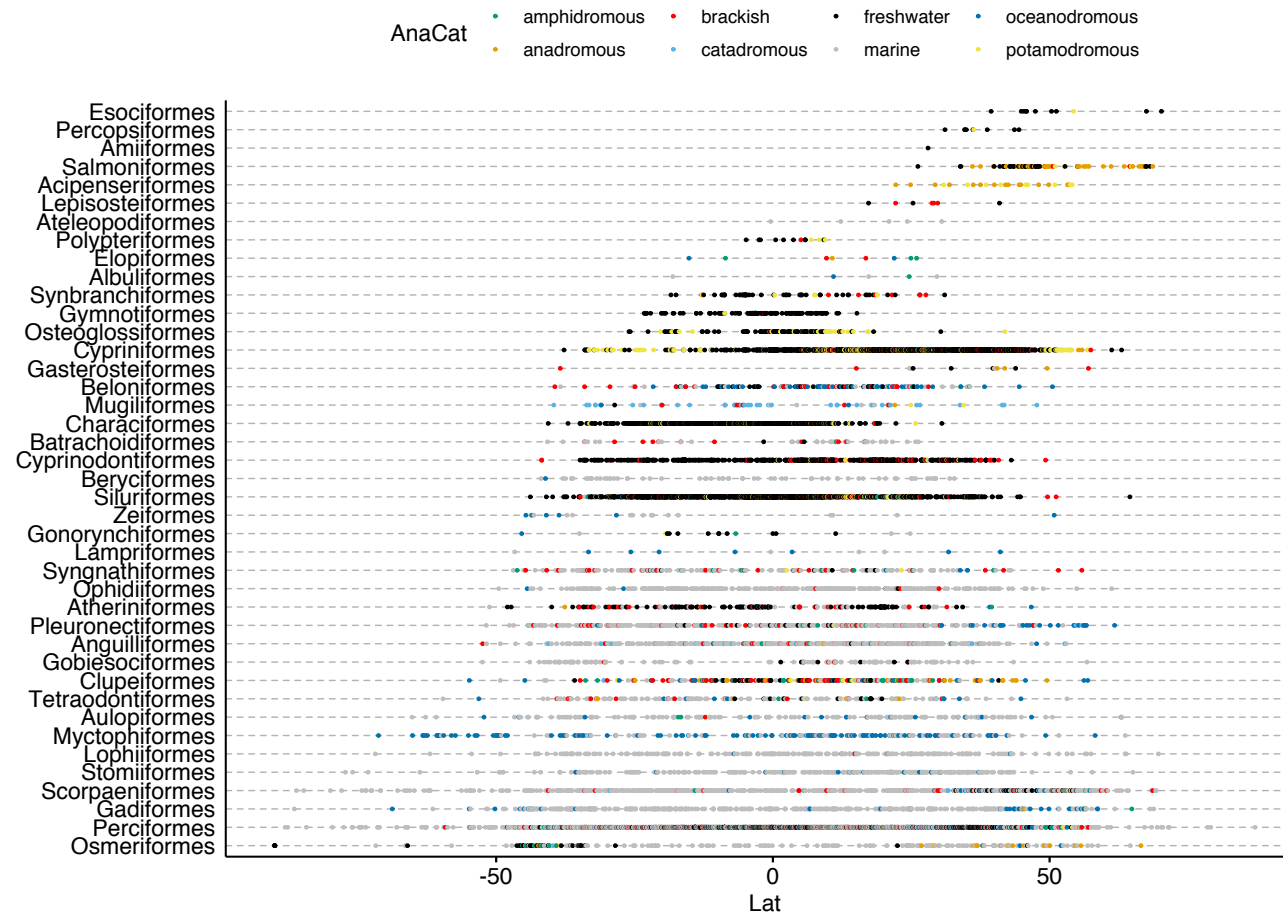
Figure S3. Dot chart of Order, midpoint latitude and life-history strategies

REFERENCES

Abell R, Thieme ML, Revenga C, et al (2008a) Freshwater Ecoregions of the World: A New Map of Biogeographic Units for Freshwater Biodiversity Conservation. Bioscience 58:403. doi: 10.1641/B580507

Abell R, Thieme ML, Revenga C, et al (2008b) Freshwater Ecoregions of the World : A New Map of Biogeo- graphic Units for Freshwater Biodiversity Conservation.

Albert JS, Reis RE (2011) Historical Biogeography of Neotropical Freshwater Fishes. University of California Press, Berkeley, California

Alerstam T, Hedenström A, Åkesson S (2003) Long-distance migration: evolution and determinants. Oikos 2:247–260.

Allen AP, Brown JH, Gillooly JF (2002) Global Biodiversity , Biochemical Kinetics , and the Energetic-Equivalence Rule. Science (80-) 297:1545–1548. doi: 10.1126/science.1072380

Allen AP, Gillooly JF, Savage VM, Brown JH (2006) Kinetic effects of temperature on rates of genetic divergence and speciation. Proc Natl Acad Sci U S A 103:9130–9135. doi: 10.1073/pnas.0603587103

Allen GH, Pavelsky TM (2018) Global extent of rivers and streams. Science (80-) 588:585–588. doi: 10.1126/science.aat0636

Alò D, Correa C, Arias C, Cárdenas L (2013) Diversity of Aplochiton Fishes (Galaxiidea) and the Taxonomic Resurrection of *A. marinus*. PLoS One 8:e71577. doi: 10.1371/journal.pone.0071577

Alò D, Correa C, Samaniego H, et al (2019) Otolith microchemistry and diadromy in Patagonian river fishes. PeerJ. doi: 10.1101/174656

Alò D, Turner TF (2005) Effects of Habitat Fragmentation on Effective Population Size in the Endangered Rio Grande Silvery Minnow. Conserv Biol 19:1138–1148. doi: 10.1111/j.1523-1739.2005.00081.x

Altshuler DL, Dudley R, Integrative S, et al (2016) The Physiology and Biomechanics of Avian Flight at High Altitude Stable URL : http://www.jstor.org/stable/3884977 REFERENCES Linked references are available on JSTOR for this article : The physiology and biomechanics of avian flight at high altitude. 46:62–71.

Araya M, Niklitschek EJ, Secor DH, Piccoli PM (2014) Partial migration in introduced wild chinook salmon (*Oncorhynchus tshawytscha*) of southern Chile. Estuar Coast Shelf Sci 149:87–95. doi: 10.1016/j.ecss.2014.07.011

Arismendi I, Nahuelhual L (2007) Non-native salmon and trout recreational fishing in lake llanquihue, Southern Chile: Economic benefits and management implications. Rev Fish Sci 15:311–325. doi: 10.1080/10641260701484655

Arismendi I, Penaluna BE, Dunham JB, et al (2014) Differential invasion success of salmonids in southern Chile: patterns and hypotheses. Rev Fish Biol Fish. doi: 10.1007/s11160-014-9351-0

Arismendi I, Soto D (2012) Are salmon-derived nutrients being incorporated in food webs of invaded streams? Evidence from southern Chile. Knowl Manag Aquat Ecosyst 405:1–6. doi: 10.1051/kmae/2012009

Arkhipkin AI, Schuchert PC, Danyushevsky L (2009) Otolith chemistry reveals fine population structure and close affinity to the Pacific and Atlantic oceanic spawning grounds in the migratory southern blue whiting (*Micromesistius australis australis*). Fish Res 96:188–194. doi: 10.1016/j.fishres.2008.11.002

Arratia F. G (1983) *Trichomycterus chungaraensis* n. sp. and *Trichomycterus laucaensis* n. sp. (Pisces, Siluriformes, Trichomycteridae) from the high Andean range. Stud Neotrop Fauna Environ 18:65–87. doi: 10.1080/01650528309360621

Arthington AH, Dulvy NK, Gladstone W, Winfield IJ (2016) Fish conservation in freshwater and marine realms: status, threats and management. Aquat Conserv Mar Freshw Ecosyst 26:838–857. doi: 10.1002/aqc.2712

Ashford JR, Jones CM, Hofmann E, et al (2005) Can otolith elemental signatures record the capture site of Patagonian toothfish (*Dissostichus eleginoides*), a fully marine fish in the Southern Ocean? Can J Fish Aquat Sci 62:2832–2840. doi: 10.1139/F05-191

Assis J, Tyberghein L, Bosh S, et al (2017) Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modelling. Glob Ecol Biogeogr 27:277–284.

Augspurger JM, Warburton M, Closs GP (2015) Life-history plasticity in amphidromous and catadromous fishes : a continuum of strategies. Rev Fish Biol Fish 27:177–192. doi: 10.1007/s11160-016-9463-9

Baerwald MR, Meek MH, Stephens MR, et al (2016) Migration-related phenotypic divergence is associated with epigenetic modifications in rainbow trout. Mol Ecol 25:1785–1800. doi: 10.1111/mec.13231

Bamber RN, Henderson PA (1988) Pre-adaptive plasticity in atherinids and the estuarine seat of teleost evolution. J Fish Biol 33:17–23. doi: 10.1111/j.1095-8649.1988.tb05554.x

Barta Z, McNamara JM, Houston AI, et al (2008) Optimal moult strategies in migratory birds. Philos Trans R Soc B Biol Sci 363:211–229. doi: 10.1098/rstb.2007.2136

Bazazi S, Romanczuk P, Thomas S, et al (2011) Nutritional state and collective motion: from individuals to mass migration. Proc R Soc B Biol Sci 278:356–363. doi:

10.1098/rspb.2010.1447

Beaulieu JM, O'Meara BC (2016) Detecting hidden diversification shifts in models of trait-dependent speciation and extinction. Syst Biol 65:583–601. doi: 10.1093/sysbio/syw022

Behrenfeld MJ, Falkowski PG (1997) Photosynthetic rates derived from satellite-based chlorophyll concentration. Limnol Oceanogr 42:1–20.

Bell CP (2000) Process in the evolution of bird migration and pattern in avian ecogeography. J. Avian Biol. 31:258–265.

Berthold P, Querner U (1981) Genetic basis of migratory behavior in European warblers. Science (80-) 212:77–79. doi: 10.1126/science.212.4490.77

Bloom DD (2013) Transitions Between Marine and Freshwaters in Fishes : Evolutionary Pattern and Process. University of Toronto

Bloom DD, Lovejoy NR (2017) On the origins of marine-derived freshwater fishes in South America. J Biogeogr 1–12. doi: 10.1111/jbi.12954

Bloom DD, Lovejoy NR (2014) The evolutionary origins of diadromy inferred from a time-calibrated phylogeny for Clupeiformes (herring and allies). Proc Biol Sci 281:20132081. doi: 10.1098/rspb.2013.2081

Boone RB, Thirgood SJ, Hopcraft JG (2006) Serengeti Wildebeest Migratory Patterns Modeled from Rainfall and New Vegetation Growth. Ecology 87:1987–1994. doi: 10.1890/0012-9658(2006)87[1987:SWMPMF]2.0.CO;2

Borcard D, Gillet F, Legendre P (2009) Numerical Ecology with R.

Börger L, Matthiopoulos J, Holdo RM, et al (2011) Migration quantified: constructing models and linking them with data. In: Animal Migration: a synthesis. pp 111–128

Borjas G (1987) Self-selection and the earnings of immigrants. Am. Econ. Rev. 77:531–553.

Breiman L, Friedman J, Stone CJ, Olshen RA (1984) Classification and regression trees. CRC Press

Brönmark C, Hulthén K, Nilsson PA, et al (2013) There and back again: migration in freshwater fishes. Can J Zool 13:1–13.

Brown JH, Gillooly JF, Allen AP, et al (2004) Toward a metabolic theory of ecology. Ecology 85:1771–1789. doi: 10.1890/03-9000

Brown JH, Lomolino M V. (1998) Biogeography, 2nd edn.

Buhl J, Sumpter DJT, Couzin ID, et al (2006) From Disorder to Order in Marching Locusts. Science (80-) 312:1402–1406. doi: 10.1126/science.1125142

Campana S (1999) Chemistry and composition of fish otoliths: pathways, mechanisms and applications. Mar Ecol Prog Ser 188:263–297.

Campana SE (2005) Otolith science entering the 21st century. Mar Freshw Res 56:485. doi: 10.1071/MF04147

Campos HC, Dazarola G, Dyer BS, et al (1998) Categorias de conservacion de peces nativos

de aguas continentales de Chile. Bol del Mus Nac Hist Nat 47:101–122.

Chamberlain S (2017) rgbif: Interface to the Global "Biodiversity" Information Facility "API".

Chang CW, Iizuka Y, Tzeng WN (2004) Migratory environmental history of the grey mullet *Mugil cephalus* as revealed by otolith Sr : Ca ratios. Mar Ecol Prog Ser 269:277–288.

Chen A, Fang J, Oswalt CM, et al (2018) Impacts of climate on the biodiversity-productivity relationship in natural forests. Nat Commun. doi: 10.1038/s41467-018-07880-w

Ciancio JE, Pascual M a., Lancelotti J, et al (2005) Natural Colonization and Establishment of a Chinook Salmon, *Oncorhynchus tshawytscha*, Population in the Santa Cruz River, an Atlantic Basin of Patagonia. Environ Biol Fishes 74:219–227. doi: 10.1007/s10641-005-0208-1

Ciancio JE, Pascual MA, Botto F, et al (2008) Stable isotope profiles of partially migratory salmonid populations in Atlantic rivers of Patagonia. J Fish Biol 72:1708–1719. doi: 10.1111/j.1095-8649.2008.01846.x

Cohen D (1967) Optimization of seasonal migratory behavior. Am Nat 101:5–17. doi: 10.1111/j.1399-3054.1989.tb05989.x

Correa-Araneda F, De Los Ríos P, Habit E (2014) Presence of the red jollytail, *Brachygalaxias bullocki* (Regan, 1908) (Galaxiformes: Galaxiidae), in freshwater forested wetlands from Chile. Rev Chil Hist Nat 87:1–4. doi: 10.1186/s40693-014-0020-4

Correa C, Bravo AP, Hendry AP (2012) Reciprocal trophic niche shifts in native and invasive fish: Salmonids and galaxiids in Patagonian lakes. Freshw Biol 57:1769–1781. doi: 10.1111/j.1365-2427.2012.02837.x

Correa C, Gross MR (2008) Chinook salmon invade southern South America. Biol Invasions 10:615–639. doi: 10.1007/s10530-007-9157-2

Correa C, Hendry AP (2012a) Invasive salmonids and lake order interact in the decline of puye grande Galaxias platei in western Patagonia lakes. Ecol Appl 22:828–842. doi: 10.1890/11-1174.1

Correa C, Hendry AP (2012b) Invasive salmonids and lake order interact in the decline of puye grande *Galaxias platei* in western Patagonia lakes. Ecol Appl 22:828–842. doi: 10.1890/11-1174.1

Cox GW (1968) The role of competition in the evolution of migration. 180–192.

Cox GW (1961) The Relation of Energy Requirements of Tropical Finches to Distribution and Migration. Ecology 42:253–266.

Cuevas C, Campos H, Busse K (1999) Cytotaxonomic studies on Chilean Galaxiid fishes. The kariotypes, C-bands, Ag-NORs and Hybrids of *Brachygalaxias gothei* and *B. bullocki* (Osteichthyes: Galaxiidae). Cytologia (Tokyo) 64:379–385.

Cusens J, Wright SD, McBride PD, Gillman LN (2012) What is the form of the productivity-

animal-species-richness relationship? a critical review and meta-analysis. Ecology 93:2241–2252.

De'ath G (2002) Multivariate regression trees: A new technique for modeling species-environment relationships. Ecology 83:1105–1117. doi: 10.1890/0012-9658(2002)083[1105:MRTANT]2.0.CO;2

de Pontual H, Lagardere F, Amara R, et al (2003) Influence of ontogenetic and environmental changes in the otolith microchemistry of juvenile sole (*Solea solea*). J Sea Res 50:199–210. doi: 10.1016/S1385-1101(03)00080-7

Diario Oficial de la Republica de Chile (2008) Tercer Proceso de Clasificacion de Especies segun su Estado de Conservacion. 39.100:4–5.

Dias MS, Oberdorff T, Hugueny B, et al (2014) Global imprint of historical connectivity on freshwater fish biodiversity. Ecol Lett 17:1130–1140. doi: 10.1111/ele.12319

Dickson KA, Graham JB (2004) Evolution and Consequences of Endothermy in Fishes. Physiol Biochem Zool 77:998–1018. doi: 10.1086/423743

Dingle H (2014) Migration: The Biology of Life on the Move, Second edi. Oxford University Press, Inc, New York

Dingle H (1980) Ecology and evolution of migration. In: Gauthreaux Jr SA (ed) Animal Migration, Orientation, and Navigation. Academic Press, London, pp 1–100

Dingle HD, Drake VA (2007) What Is Migration? Bioscience 57:113–121.

Dodson J, Laroche J, Lecomte F (2009) Contrasting evolutionary pathways of anadromy in euteleostean fishes. … Fishes a Dyn Glob … 63–77.

Dodson JJ (1997) Fish migration: an evolutionary perspective. Behav. Ecol. Teleost Fishes 10–36.

Duarte LDS, Prieto P V, Pillar VD (2012) Assessing spatial and environmental drivers of phylogenetic structure in Brazilian Araucaria forests. Ecography (Cop) 35:952–960. doi: 10.1111/j.1600-0587.2011.07193.x

Dunn NR, O'Brian LK (2007) Possible divergent reproductive strategies in New Zealand riverine non-migratory Galaxias fishes. New Zeal Nat Sci 32:13–20.

Dyer BS (2000) Systematic review and biogeography of the freshwater fishes of Chile. Estud Ocean 19:77–98.

Economo EP, Huang J-P, Fischer G, et al (2019) Evolution of the latitudinal diversity gradient in the hyperdiverse ant genus Pheidole. Glob Ecol Biogeogr. doi: 10.1111/geb.12867

Ekau W, Auel H, Portner HO, Gilbert D (2010) Impacts of hypoxia on the structure and processes in pelagic communities (zooplankton, macro-invertebrates and fish). Biogeosciences 7:1669–1699. doi: 10.5194/bg-7-1669-2010

Elsdon T, Gillanders B (2002a) Interactive effects of temperature and salinity on otolith chemistry: challenges for determining environmental histories of fish. Can J Fish Aquat Sci 59:1796–1808.

Elsdon TS, Gillanders BM (2004) Fish otolith chemistry influenced by exposure to multiple environmental variables. J Exp Mar Bio Ecol 313:269–284. doi: 10.1016/j.jembe.2004.08.010

Elsdon TS, Gillanders BM (2002b) Interactive effects of temperature and salinity on otolith chemistry: challenges for determining environmental histories of fish. Can J Fish Aquat Sci 59:1796–1808. doi: 10.1139/f02-154

ESRI (2012) ArcGIS Desktop.

FAO (2014) FAO Statistical Areas for Fishery Purposes. In: FAO Fisheries and Aquaculture Department [online]. http://www.fao.org/fishery/area/search/en. Accessed 23 Jul 2018

Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int J Climatol 37:4302–4315. doi: DOI:10.1002/joc.5086

Fitzjohn RG (2012) Diversitree: Comparative phylogenetic analyses of diversification in R. Methods Ecol Evol 3:1084–1092. doi: 10.1111/j.2041-210X.2012.00234.x

Fowler AJ, Campana SE, Jones CM, Thorrold SR (1995) Experimental assessment of the effect of temperature and salinity on elemental composition of otoliths using laser ablation ICPMS. Can J Fish Aquat Sci 52:1431–1441.

Fretwell SD (1972) Populations in a Seasonal Environment. Princeton, New Jersey

Fretwell SD, Lucas HL (1969) On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheor. 19:37–44.

Friedman NR, Harmáčková L, Economo EP, Remeš V (2017) Smaller beaks for colder winters: Thermoregulation drives beak size evolution in Australasian songbirds. Evolution (N Y) 71:2120–2129. doi: 10.1111/evo.13274

Fryxell JM, Wilmshurst JF, Sinclair a. RE (2004) Predictive models of movement by serengeti grazers. Ecology 85:2429–2435. doi: 10.1890/04-0147

Fryxell M, Sinclair ARE (1988) Causes and Consequences of Migration by Large Herbivores.

Fullerton AH, Burnett KM, Steel EA, et al (2010) Hydrological connectivity for riverine fish: measurement challenges and research opportunities. Freshw Biol 55:2215–2237. doi: 10.1111/j.1365-2427.2010.02448.x

Garcia-Rosello E, Guisande C, Manjarres-Hernandez A, et al (2015) Can we derive macroecological patterns from primary Global Biodiversity Information Facility data? Glob Ecol Biogeogr 24:335–347. doi: 10.1111/geb.12260

Garcia A, Jorde K, Habit EM, et al (2011) Downstream Environmental Effects of Dam Operations: Changes in Habitat Quality for Native Fish Species. 27:312–327. doi: 10.1002/rra

Gaston KJ (2000) Global patterns in biodiversity. Nature 405:220–7. doi: 10.1038/35012228

Gillanders BM (2005) Using elemental chemistry of fish otoliths to determine connectivity between estuarine and coastal habitats. Estuar Coast Shelf Sci 64:47–57. doi: 10.1016/j.ecss.2005.02.005

Gillanders BM, Izzo C, Doubleday ZA, Ye Q (2015) Partial migration: Growth varies between resident and migratory fish. Biol Lett. doi: 10.1098/rsbl.2014.0850

Gillooly JF, Allen AP, West GB, Brown JH (2005) The rate of DNA evolution: effects of body size and temperature on the molecular clock. Proc Natl Acad Sci U S A 102:140–145. doi: 10.1073/pnas.0407735101

Gillooly JF, Brown JH, West GB, et al (2001) Effects of Size and Temperature on Metabolic Rate. 293:2248–2251.

González-Wevar C, Salinas P, Hüne M, et al (2015) Contrasting Genetic Structure and Diversity of Galaxias maculatus (Jenyns, 1848) Along the Chilean Coast: Stock Identification for Fishery Management. J Hered 106:439–447. doi: 10.1093/jhered/esv005

Gonzalez EG, Beerli P, Zardoya R (2008) Genetic structuring and migration patterns of Atlantic bigeye tuna, Thunnus obesus (Lowe, 1839). BMC Evol Biol 8:252. doi: 10.1186/1471-2148-8-252

Górski K, González J, Vivancos A, et al (2016) Young-of-the-year Coho Salmon *Oncorhynchus kisutch* recruit in fresh waters of remote Patagonian fjords in southern Chile (51 ° S). Biol Invasions. doi: 10.1007/s10530-016-1341-9

Górski K, Habit EM, Pingram MA, Manosalva AJ (2015) Variation of the use of marine resources by *Galaxias maculatus* in large Chilean rivers. Hydrobiologia. doi: 10.1007/s10750-015-2542-4

Griffiths D (2015) Connectivity and vagility determine spatial richness gradients and diversification of freshwater fish in North America and Europe. Biol J Linn Soc 116:773–786. doi: 10.1111/bij.12638

Griswold CK, Taylor CM, Norris DR (2010) The evolution of migration in a seasonal environment. Proc R Soc B Biol Sci 277:2711–2720. doi: 10.1098/rspb.2010.0550

Gross MR (1987) Evolution of diadromy in fishes. Am Fish Soc Symp 1:14–25.

Gross MR, Coleman RM, McDowall RM (1988) Aquatic Productivity and the Evolution of Diadromous Fish Migration. Science (80-) 239:1291–1293.

Guan W, Bol P, Lewis B, et al (2012) WorldMap–a geospatial framework for collaborative research. Ann GIS 18:121–134.

Habit E, Dyer BS, Vila I (2006) Current state of knowledge of freshwater fishes of Chile. Gayana 70:100–113.

Habit E, Gonzalez J, Ruzzante DE, Walde SJ (2012) Native and introduced fish species richness in Chilean Patagonian lakes: Inferences on invasion mechanisms using salmonid-free lakes. Divers Distrib 18:1153–1165. doi: 10.1111/j.1472-4642.2012.00906.x

Habit EM, Victoriano P (2005) Peces de agua dulce de la Cordillera de la Costa. In: Smith-Ramírez C, Armesto J, Valdovinos C (eds) Biodiversidad y Ecología de la Cordillera de

la Costa de Chile. Editorial Universitaria Bosque Nativo, Santiago de Chile, pp 374–389

Halden NM, Mejia SR, Babaluk JA, et al (2000) Oscillatory zinc distribution in Arctic char (Salvelinus alpinus) otoliths : The result of biology or environment? Fish Res 46:289–298.

Hecht BC, Thrower FP, Hale MC, et al (2012) Genetic Architecture of Migration-Related Traits in Rainbow and Steelhead Trout, Oncorhynchus mykiss. G3&#58; Genes|Genomes|Genetics 2:1113–1127. doi: 10.1534/g3.112.003137

Helfield JM, Naiman RJ (2001) Effects of Salmon-Derived Nitrogen on Riparian Forest Growth and Implications for Stream Productivity. Ecology 82:2403–2409.

Henseler J, Sarstedt M (2013) Goodness-of-fit indices for partial least squares path modeling. Comput Stat 28:565–580. doi: 10.1007/s00180-012-0317-1

Herrera-Alsina L, Van Els P, Etienne RS (2018) Detecting the Dependence of Diversification on Multiple Traits from Phylogenetic Trees and Trait Data. Syst Biol 68:317–328. doi: 10.1093/sysbio/syy057

Hicks AS, Closs GP, Swearer SE (2010) Otolith microchemistry of two amphidromous galaxiids across an experimental salinity gradient: A multi-element approach for tracking diadromous migrations. J Exp Mar Bio Ecol 394:86–97. doi: 10.1016/j.jembe.2010.07.018

Hillebrand H (2004) On the Generality of the Latitudinal Diversity Gradient. Am Nat 163:284–290. doi: 10.1086/381004

Holt RD, Fryxell JM (2011) Theoretical reflections on the evolution of migration. In: Animal Migration: a synthesis. pp 17–31

Howland KL, Tonn WM, Babaluk J a., Tallman RF (2001) Identification of Freshwater and Anadromous Inconnu in the Mackenzie River System by Analysis of Otolith Strontium. Trans Am Fish Soc 130:725–741. doi: 10.1577/1548-8659(2001)130<0725:IOFAAI>2.0.CO;2

Instituto Nacional de Estadisticas (2015) Caracteristicas generales de los principales rios de Chile. In: Inf. Medio Ambient. http://historico.ine.cl/medioambiente/descargas/2015/xls/CAP5_AGUA.xlsx.

IUCN (2015) The IUCN Red List of Threatened Species. www.iucnredlist.org. Accessed 13 May 2016

Joo Y-J, Kim CS, Yoo S-H (2015) Energy Consumption, Co2 Emission, and Economic Growth: Evidence from Chile. Int J Green Energy 12:543–550. doi: 10.1080/15435075.2013.834822

Joseph L, Lessa EP, Christidis L (1999) Phylogeny and biogeography in the evolution of migration: shorebirds of the *Charadrius* complex. J Biogeogr 26:329–342.

Kaitala A, Kaitala V, Lundberg P (1993) A theory of partial migration. Am Nat 142:59. doi: 10.1086/285529

Kalish JM (1990) Use of Otolith Microchemistry to Distinguish the Progeny of Sympatric Anadromous and Non-anadromous Salmonids. Fish Bull (Wash DC) 88:657–666.

Kaschner K, Ready JS, Agbayani E, et al (2008) AquaMaps Environmental Dataset: Half-Degree Cells Authority File (HCAF). In: World Wide Web Electron. Publ.

Kokko H, Lundberg P (2001) Dispersal , Migration , and Offspring Retention in Saturated Habitats. Am Nat 157:188–202.

Kraus R (2004) Incorporation of strontium into otoliths of an estuarine fish. J Exp Mar Bio Ecol 302:85–106. doi: 10.1016/j.jembe.2003.10.004

L'opez-de-Lacalle (2016) tsoutliers: Detection of Outliers in Time Series.

Laborde A, Gonzalez A, Sanhueza C, et al (2016) Hydropower Development, Riverine Connectivity, and Non-sport Fish Species: criteria for Hydraulic Design of Fishways. River Res Appl 32:1949–1957.

Lack D (1954) The natural regulation of animal numbers. Oxford University Press

Lack D (1968) Bird Migration and Natural Selection. Oikos 19:1–9. doi: 10.2307/3564725

Lampert W (1989) The adaptive significance of diel Vertical Migration of Zooplankton. 3:21–27.

Lee CE, Bell M a (1999) Causes and consequences of freshwater invasions. Trends Ecol Evol 14:284–288.

Legendre P, Legendre L (1998) Numerical ecology. Elsevier Science

Leibold MA (1999) Biodiversity and nutrient enrichment in pond plankton communities. Evol Ecol Res 1:73–95.

Lévêque C, Oberdorff T, Paugy D, et al (2008) Global diversity of fish (Pisces) in freshwater. Hydrobiologia 595:545–567. doi: 10.1007/s10750-007-9034-0

Limburg KE (1995) Otolith strontium traces environmental history of subyearling American shad *Alosa sapidissima*. Mar Ecol Prog Ser 119:25–35. doi: 10.3354/meps119025

Limburg KE, Landergren P, Westin L, et al (2001) Flexible modes of anadromy in Baltic sea trout : making the most of marginal spawning streams. J Fish Biol 59:682–695. doi: 10.1006/jfbi.2001.1681

Louchart A (2008) Emergence of long distance bird migrations: A new model integrating global climate changes. Naturwissenschaften 95:1109–1119. doi: 10.1007/s00114-008-0435-3

Lundberg P (1987) Partial bird migration and evolutionarily stable strategies. J Theor Biol 125:351–360. doi: 10.1016/S0022-5193(87)80067-X

Lundberg P (2013) On the evolutionary stability of partial migration. J Theor Biol 321:36–39. doi: 10.1016/j.jtbi.2012.12.017

Mangel M (1994) Climate-Change and Salmonid Life-History Variation. Deep Res Part Ii-Topical Stud Oceanogr 41:75–106.

Marín VH, Tironi A, Alejandra M, Contreras M (2013) Modeling suspended solids in a Northern Chilean Patagonia glacier-fed fjord : GLOF scenarios under climate change conditions. Ecol Modell 264:7–16. doi: 10.1016/j.ecolmodel.2012.06.017

Maynard Smith J (1982) Evolution and the Theory of Games. Cambridge University Press

McDowall RM (1997) The evolution of diadromy in fishes (revisited) and its place in phylogenetic analysis. Rev Fish Biol Fish 7:443–462. doi: 10.1023/A:1018404331601

McDowall RM (1988) Diadromy in Fishes. Timber Press, Portland, Oregon

McDowall RM (1992) Diadromy : Origins and Definitions of Terminology. Copeia 1992:248–251.

McDowall RM (2002a) Accumulating evidence for a dispersal biogeography of southern cool temperate freshwater fishes. J Biogeogr 29:207–219. doi: 10.1046/j.1365-2699.2002.00670.x

McDowall RM (1971) The galaxiid fishes of South America. Zool J Linn Soc 50:33–73. doi: 10.1111/j.1096-3642.1971.tb00751.x

McDowall RM (2002b) The origin of salmonid fishes: Marine, freshwater ... or neither? Rev Fish Biol Fish 11:171–179. doi: 10.1023/A:1020370328194

McDowall RM (2001) Diadromy, diversity and divergence: Implications for speciation processes in fishes. Fish Fish 2:278–285. doi: 10.1046/j.1467-2960.2001.00050.x

McDowall RM (1987) The occurrence and distribution of diadromy among fishes.

McDowall RM (2007) On amphidromy, a distinct form of diadromy in aquatic organisms. Fish Fish 8:1–13. doi: 10.1111/j.1467-2979.2007.00232.x

McDowall RM (2008) Why are so many boreal freshwater fishes anadromous? Confronting'conventional wisdom'. Fish Fish 9:208–213. doi: 10.1111/j.1467-2979.2008.00271.x

McDowall RM (2002c) Accumulating evidence for a dispersal biogeography of southern cool temperate freshwater fishes. J. Biogeogr. 29:207–219.

McLaren I (1963) Effects of temperature on growth of zooplankton, and the adaptive value of vertical migration. J Fish Board Canada 20:685–727. doi: 10.1139/f63-046

Miles NG (2007) Biology and ecology of diadromous fishes in south eastern Australia. University of Wollongong

Milner-Gulland EJ, Fryxell JM, Sinclair ARE (2011) Animal migration: a synthesis. In: Milner-Gulland EJ, Fryxell JM, Sinclair ARE (eds) Animal migration. Oxford University Press, New York,

Ministerio del Medio Ambiente (2013) Especies: Clasificacion segun estado de conservacion. http://www.mma.gob.cl/clasificacionespecies/doc/UNIFICADA_de_Especie_Estado_Conservacion_Nov2014_publico.xls.

Mittelbach GG, Schemske DW, Cornell H V., et al (2007) Evolution and the latitudinal

diversity gradient: Speciation, extinction and biogeography. Ecol Lett 10:315–331. doi: 10.1111/j.1461-0248.2007.01020.x

Mittelbach GG, Steiner CF, Scheiner SM, et al (2001) What is the observed relationship between species richness and productivity? Ecology 82:2381–2396. doi: 10.1890/0012-9658(2001)082[2381:WITORB]2.0.CO;2

Mueller T, Fagan WF (2008) Search and navgation in dynamic environments - from individual behaviours to population distributions. Oikos 117:654–664. doi: 10.1111/j.2008.0030-1299.16291.x

Munoz-Ramirez C, Jara A, Beltran-Concha M, et al (2010) Distribucion de la familia Diplomystidae (Pisces: Siluriformes) en Chile: Nuevos Registros. Bol Biodivers Chile 4:6–17.

Murillo & Ruiz (2002) El Puye *Galaxias Globiceps*. Gayana 66:191–197. doi: 10.13140/RG.2.1.5180.0481

Myers GS (1949) Usage of anadromous, catadromous and allied terms for migratory fishes. Copeia 1949:89–97.

Nathan R, Getz WM, Revilla E, et al (2008) A movement ecology paradigm for unifying organismal movement research. Proc Natl Acad Sci U S A 105:19052–9. doi: 10.1073/pnas.0800375105

Neira FJ, Bradley JS, Potter IC, Hilliard RW (1988) Morphological variation among widely dispersed larval populations of anadromous southern hemisphere lampreys (Geotriidae and Mordaciidae). Zool J Linn Soc 92:383–408. doi: 10.1111/j.1096-3642.1988.tb01730.x

Nelson JS (2006a) Fishes of the World. Wiley

Nelson JS (2006b) Fishes of the world, 4th edn. John Wiley & Sons Inc, Hoboken, New Jersey

Nordeng H (1983) Solution to the 'char problem' based on Arctic char (*Salvelinus alpinus*) in Norway. Can J Fish Aquat Sci 40:372–87. doi: 10.1139/f83-159

Norman J, Greenwood P (1975) A History of Fishes, third revi. E. Benn, London

Northcote TG (1997) Potamodromy in Salmonidae - living and moving in the fast lane. North Am J Fish Manag 1029–1045. doi: http://www.tandfonline.com/action/showCitFormats?doi=10.1577/1548-8675(1997)017%3C1029:PISAMI%3E2.3.CO;2

Oberdorff T, Hugueny B, Guegan J-F (1997) Is there an influence of historical events on contemporary fish species richness in rivers? Comparisons between Western Europe and North America. J Biogeogr 24:461–467. doi: 10.1111/j.1365-2699.1997.00113.x

Oksanen J, Blanchet GF, Friendly M, et al (2017) vegan: Community Ecology Package.

Olson D, Dinerstein E, Wikramanayake E, et al (2001) Terrestrial ecoregions of the world: a new map of life on Earth. Bioscience 51:933–938.

Oregon State (2017) Ocean Productivity.

Paradis E, Claude J, Strimmer K (2004) APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20:289–290.

Pardo R, Scott S, Vila I (2005) Analisis de formas en especies Chilenas del generoTrichomycterus (Osteichthyes: Siluriformes) utilizando morfometria geometrica. Gayana (Concepción) 69:180–183. doi: 10.4067/S0717-65382005000100023

Penaluna BE, Arismendi I, Soto D (2009) Evidence of Interactive Segregation between Introduced Trout and Native Fishes in Northern Patagonian Rivers, Chile. Trans Am Fish Soc 138:839–845. doi: 10.1577/T08-134.1

Pillar VD, Duarte L d. S (2010) A framework for metacommunity analysis of phylogenetic structure. Ecol Lett 13:587–596. doi: 10.1111/j.1461-0248.2010.01456.x

Porch CE (2005) The sutainability of western Atlantic bluefin tuna: a warm blooded fish in a hot blooded fishery. Bull Mar Sci 76:363–384.

Porto C (2015) World Hydrography. Orogénesis Soluciones Geográficas. Based on shapes from Enviromental Systems Research Institute (ESRI).

Pracheil BM, Hogan JD, Lyons J, McIntyre PB (2014) Using Hard-Part Microchemistry to Advance Conservation and Management of North American Freshwater Fishes. Fisheries 39:451–465. doi: 10.1080/03632415.2014.937858

Prieto M, Bauer C (2012) Hydroelectric power generation in Chile : an institutional critique of the neutrality of market mechanisms. Water Int 37:131–146. doi: 10.1080/02508060.2012.662731

Proctor CH, Thresher RE (1998) Effects of specimen handling and otolith preparation on concentration of elements in fish otoliths. Mar Biol 131:681–694. doi: 10.1007/s002270050360

Pulido F (2011) Evolutionary genetics of partial migration - the threshold model of migration revis(it)ed. Oikos 120:1776–1783. doi: 10.1111/j.1600-0706.2011.19844.x

Pulido F (2007) The Genetics and Evolution of Avian Migration. Bio Sci 57:165–174.

Pulido F, Berthold P, van Noordwijk AJ (1996) Frequency of migrants and migratory activity are genetically correlated in a bird population: evolutionary implications. Proc Natl Acad Sci U S A 93:14642–14647. doi: 10.1073/pnas.93.25.14642

Quinn TP (2005) Pacific salmon and trout. University of Washington Press

R Core Team (2017) R: A language and environment for statistical computing.

Rabosky DL, Chang J, Title PO, et al (2018) An inverse latitudinal gradient in speciation rate for marine fishes. Nature 559:392–395. doi: 10.1038/s41586-018-0273-1

Rabosky DL, Goldberg EE (2015) Model inadequacy and mistaken inferences of trait-dependent speciation. Syst Biol 64:340–355. doi: 10.1093/sysbio/syu131

Rabosky DL, Grundler M, Anderson C, et al (2014) BAMMtools: An R package for the analysis of evolutionary dynamics on phylogenetic trees. Methods Ecol Evol 5:701–707. doi: 10.1111/2041-210X.12199

Rabosky DL, Huang H (2016) A Robust Semi-Parametric Test for Detecting Trait-Dependent Diversification. Syst Biol 65:181–193. doi: 10.1093/sysbio/syv066

Rabosky DL, Title PO, Huang H (2015) Minimal effects of latitude on present-day speciation rates in New World birds. Proc R Soc B Biol Sci. doi: 10.1098/rspb.2014.2889

Radinger J, Wolter C (2014) Patterns and predictors of fish dispersal in rivers. Fish Fish 15:456–473. doi: 10.1111/faf.12028

Railsback SF, Grimm V (2012) Agent-Based and Individual-Based Modeling. Princeton University Press, Princeton, New Jersey

Redding DW, Mooers AØ (2006) Incorporating Evolutionary Measures into Conservation Prioritization. Conserv Biol 20:1670–1678. doi: 10.1111/j.1523-1739.2006.00555.x

Reluga TC, Shaw AK (2015) Resource distribution drives the adoption of migratory, partially migratory, or residential strategies. Theor Ecol 8:437–447. doi: 10.1007/s12080-015-0263-y

Riva-Rossi C, Pascual MA, Babaluk JA, et al (2007) Intra-population variation in anadromy and reproductive life span in rainbow trout introduced in the Santa Cruz River, Argentina. J Fish Biol 70:1780–1797.

Roff D (1990) The Evolution of Flightlessness. Ecol Monogr 60:389–421.

Rohde K (1992) Latitudinal Gradients In Species-diversity - the Search For the Primary Cause. Oikos 65:514–527. doi: 10.2307/3545569

Romanczuk P, Couzin ID, Schimansky-Geier L (2008) Collective Motion due to escape and pursuit response. 1–5. doi: 10.1103/PhysRevLett.102.010602

Ruiz-Jarabo I, Gonzalez-Wevar CA, Oyarzun R, et al (2016) Isolation driven divergence in osmoregulation in Galaxias maculatus (Jenyns, 1848) (Actinopterygii: Osmeriformes). PLoS One 11:1–21. doi: 10.1371/journal.pone.0154766

Ruzzante DE, Walde SJ, Cussac VE, et al (2006) Phylogeography of the Percichthyidae (Pisces) in Patagonia: roles of orogeny, glaciation, and volcanism. Mol Ecol 15:2949–68. doi: 10.1111/j.1365-294X.2006.03010.x

Ruzzante DE, Walde SJ, Gosse JC, et al (2008) Climate control on ancestral population dynamics: insight from Patagonian fish phylogeography. Mol Ecol 17:2234–44. doi: 10.1111/j.1365-294X.2008.03738.x

Salas D, Veliz D, Scott S (2012) Diferenciación morfológica en especies del género Cheirodon (Ostariophysi : Characidae) mediante morfometría tradicional y geométrica. 76:142–152.

Sanchez G (2013) PLS Path Modeling with R. R Packag Notes 235. doi: citeulike-article-id:13341888

Santana C, Falvey M, Ibarra M, Garcia M (2014) Energias Renovables en Chile. El potencial eolico, solar e hidroelectrico de Arica a Chiloe. MINENERGIA/GIZ, Santiago de Chile

Satterthwaite WH, Beakes MP, Collins EM, et al (2009) Steelhead Life History on

California's Central Coast: Insights from a State-Dependent Model. Trans Am Fish Soc 138:532–548. doi: 10.1577/T08-164.1

Schultz ET, McCormick SD (2013) Euryhalinity in An Evolutionary Context. In: EURYHALINE FISHES. Fish Physiology. Elsevier, Amsterdam (The Netherlands) and Boston (Massachusetts), pp 477–533

Secor DH, Rooker JR (2000) Is otolith strontium a useful scalar of life cycles in estuarine fishes ? Fish Res 46:359–371.

Seibert HC (1949) Differences between migrant and non-migrant birds in food and water intake at various temperatures and photoperiods. Auk 66:128–153.

Shipley B (2016) Cause and Correlation in Biology, Second. Cambridge University Press, Cambridge

Simpson SJ, Sword G a. (2009) Phase polyphenism in locusts: mechanisms, population consequences, adaptive significance and evolution. In: Whitman DW, Ananthakrishnan TN (eds) Phenotypic plasticity of insects: mechanisms and consequences. Taylor & Francis Group, pp 147–189

Simpson SJ, Sword G a, Lorch PD, Couzin ID (2006) Cannibal crickets on a forced march for protein and salt. Proc Natl Acad Sci U S A 103:4152–4156. doi: 10.1073/pnas.0508915103

Sjaastad LA (1962) The Costs and Returns of Human Migration. J Polit Econ 70:80–93.

Southwood T (1962) Migration of terrestrial arthropods in relation to habitat. Biol Rev 37:171–211.

Southwood T (1977) Habitat, the templet for ecological strategies? J Anim Ecol 46:337–365. doi: 10.2307/3817

Spalding MD, Agostini VN, Rice J, Grant SM (2012) Pelagic provinces of the world: A biogeographic classification of the world's surface pelagic waters. Ocean Coast Manag 60:19–30. doi: 10.1016/j.ocecoaman.2011.12.016

Spalding MD, FOX HE, ALLEN GR, et al (2007) Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas. Bioscience 57:573. doi: 10.1641/B570707

Stover KK, Burnett KG, McElroy EJ, Burnett LE (2013) Locomotory fatigue and size in the Atlantic blue crab, Callinectes sapidus. Biol Bull 224:63–67.

Strobl C (2009) An Introduction to Recursive Partitioning: Rationale, Application and Characteristics of Classification and Regression Trees, Bagging and Random Forests. Psychol Methods 14:323–348. doi: 10.1037/a0016973.An

Sturgeon RE, Willie SN, Yang L, et al (2005) Certification of a fish otolith reference material in support of quality assurance for trace element analysis. J Anal At Spectrom 20:1067–1071. doi: 10.1039/b503655k

Sturrock AM, Hunter E, Milton JA, et al (2015) Quantifying physiological influences on otolith microchemistry. Methods Ecol Evol 6:806–816. doi: 10.1111/2041-210X.12381

Svenning J-C, Eiserhardt WL, Normand S, et al (2015) The Influence of Paleoclimate on Present-Day Patterns in Biodiversity and Ecosystems. Annu Rev Ecol Evol Syst 46:551–572. doi: 10.1146/annurev-ecolsys-112414-054314

Sword GA, Lorch PD, Gwynne DT (2005) Insect behaviour: Migratory bands give crickets protection. Nature 433:703. doi: 10.1038/433703a

Therneau TM, Atkinson EJ (1997) An Introduction to Recusive Partitioning Using the RPART Routines. Mayo Found Tech Rep 1–62.

Toledo HR (2014) Ecología política y represas : elementos para el análisis del Proyecto HidroAysén en la Patagonia chilena 1. Rev Geogr Norte Gd 57:161–175.

Tsukamoto K, Miller M, Kotake A, et al (2009) The origin of fish migration: The random escapement hypothesis. In: Haro AJ, Smith KL, Rulifson RA, et al. (eds) Challenges for diadromous fishes in a dynamic global environment. American Fisheries Society Symposium 69, Bethesda, MD, pp 45–61

Tsuzuki MY, Strüssmann CA, Takashima F (2008) Effect of salinity on the oxygen consumption of larvae of the silversides *Odontesthes hatcheria* and *O. bonariensis* (Osteichthyes, Atherinopsidae). Brazilian Arch Biol Technol 51:563–567. doi: 10.1590/S1516-89132008000300017

Tyberghein L, Verbruggen H, Pauly K, et al (2012) Bio-ORACLE: a global environmental dataset for marine species distribution modelling. Glob Ecol Biogeogr 21:272–281. doi: DOI: 10.1111/j.1466-8238.2011.00656.x

Tzeng WN, Severin KP, Wickstrom H (1997) Use of otolith microchemistry to investigate the environmental history of European eel *Anguilla anguilla*. Mar Ecol Ser 149:73–81. doi: 10.3354/meps149073

Tzeng WN, Tsai YC (1994) Changes in otolith microchemistry of the japanese eel, _Anguilla japonica_, during its migration from the ocean to the river of Taiwan. J Fish Biol 45:671–683.

Unmack PJ (2001) Biogeography of Australian freshwater fishes. J Biogeogr 28:1053–1089. doi: 10.1046/j.1365-2699.2001.00615.x

Unmack PJ, Barriga JP, Battini M a., et al (2012) Phylogeography of the catfish *Hatcheria macraei* reveals a negligible role of drainage divides in structuring populations. Mol Ecol 21:942–959. doi: 10.1111/j.1365-294X.2011.05408.x

Unmack PJ, Bennin AP, Habit EM, et al (2009) Impact of ocean barriers, topography, and glaciation on the phylogeography of the catfish *Trichomycterus areolatus* (Teleostei: Trichomycteridae) in Chile. Biol J Linn Soc 97:876–892. doi: 10.1111/j.1095-8312.2009.01224.x

Valdovinos C, Navarrete SA, Marquet PA (2003) Mollusk species diversity in the Southeastern Pacific: Why are there more species towards the pole? Ecography (Cop) 26:139–144. doi: 10.1034/j.1600-0587.2003.03349.x

van der Windt DA, Duarte LDS (2014) PCPS – an R-package for exploring phylogenetic

eigenvectors across metacommunities. Front Biogeogr 6:144–148. doi: 10.21425/F5FBG22943

van Noordwijk AJ, Pulido F, Helm B, et al (2006) A framework for the study of genetic variation in migratory behaviour. J Ornithol 147:221–233. doi: 10.1007/s10336-005-0047-z

Vanhaecke D, Garcia de Leaniz C, Gajardo G, et al (2012) DNA barcoding and microsatellites help species delimitation and hybrid identification in endangered galaxiid fishes. PLoS One 7:e32939. doi: 10.1371/journal.pone.0032939

Vargas CA, Aguayo M, Torres R (2011) Allochthonous subsidies of organic matter across a lake – river – fjord landscape in the Chilean Patagonia: Implications for marine zooplankton in inner fjord areas. Cont Shelf Res 31:187–201. doi: 10.1016/j.csr.2010.06.016

Vargas P V., Arismendi I, Gomez-Uchida D (2015) Evaluating taxonomic homogenization of freshwater fish assemblages in Chile. Rev Chil Hist Nat. doi: 10.1186/s40693-015-0046-2

Vellend M, Cornwell WK, Magnuson-ford K, Mooers AØ (2010) Measuring phylogenetic biodiversity. In: Biological diversity: frontiers in measurement and assessment. Oxford University Press, pp 193–206

Vigliano PH, Alonso MF, Aquaculture M (2007) Salmonid Introductions in Patagonia: A Mixed Blessing. Springer Netherlands, Dordrecht

Vignon M (2015) Extracting environmental histories from sclerochronological structures - Recursive partitioning as a mean to explore multielemental composition of fish otolith. Ecol Inform 30:159–169.

Vila I (2006) A New Species of Killifish in the Genus Orestias (Teleostei: Cyprinodontidae) from the Southern High Andes, Chile. Copeia 2006:472–477. doi: 10.1643/0045-8511(2006)2006[472:ANSOKI]2.0.CO;2

Vila I, Mendez MA, Scott S, et al (2007) Threatened fishes of the world: *Orestias ascotanensis* Parenti, 1984 (Cyprinodontidae). Environ Biol Fishes 80:491–492. doi: 10.1007/s10641-006-9150-0

Vila I, Scott S, Mendez MA, et al (2011) *Orestias gloriae*, a new species of cyprinodontid fish from saltpan spring of the southern high Andes (Teleostei: Cyprinodontidae). Ichthyol Explor Freshwaters 22:345–353.

Vinzi VE, Chin WW, Henseler J, H W (eds) (2011) Handbook of Partial Least Squares, Springer H. Springer

Volk EC, Blakley A, Schroder SL, Kuehner SM (2000) Otolith chemistry reflects migratory characteristics of Pacific salmonids: Using otolith core chemistry to distinguish maternal associations with sea and freshwaters. Fish Res 46:251–266. doi: 10.1016/S0165-7836(00)00150-8

von Haartman L (1968) The evolution of resident versus migratory habit in birds. Some

considerations. Ornis Fenn 45:1–7.

Wagenmakers E, Farrel S (2004) AIC model selection using Akaike weights. Psychon Bull Rev 11:192–196. doi: 10.1021/ef300604q

Waples RS, Zabel RW, Scheuerell MD, Sanderson BL (2007) Evolutionary responses by native species to major anthropogenic changes to their ecosystems: Pacific salmon in the Columbia River hydropower system. Mol Ecol 17:84–96. doi: 10.1111/j.1365-294X.2007.03510.x

Waters JM, Dijkstra LH, Wallis GP (2000) Biogeography of a southern hemisphere freshwater fish: How important is marine dispersal. Mol Ecol 9:1815–1821. doi: 10.1046/j.1365-294X.2000.01082.x

Wegner NC, Snodgrass OE, Dewar H, Hyde JR (2015) Whole-body endothermy in a mesopelagic fish, the opah, Lampris guttatus. Science (80-) 348:786–789. doi: 10.1126/science.aaa8902

Wells BK, Rieman BE, Clayton JL, et al (2003) Relationships between water, otolith, and scale chemistries of Westslope Cutthroat Trout from the Coeur d'Alene River, Idaho: the potential application of hard-part chemistry to describe movements in freshwater. Trans Am Fish Soc 132:409–424.

West GC (1960) Seasonal variation in the energy balance of the tree sparrow in relation to migration. Auk 77:306–329.

Wilkes M, Baumgartner L, Boys C, et al (2018) Fish-Net: Probabilistic models for fishway planning, design and monitoring to support environmentally sustainable hydropower. Fish Fish 19:677–697. doi: 10.1111/faf.12282

Wilkes M, Mckenzie M, Webb JA (2017) Fish passage design for sustainable hydropower in the temperate Southern Hemisphere: an evidence review. Rev Fish Biol Fish 1–19.

Winemiller KO, Jepsen DB (1998) Effects of seasonality and fish movement on tropical river food webs. J Fish Biol 53:267–296. doi: 10.1111/j.1095-8649.1998.tb01032.x

Wolff BS, Johnson BM, Landress CM (2013) Classification of hatchery and wild fish using natural geochemical signatures in otoliths, fin rays, and scales of an endangered catostomid. Can J Fish Aquat Sci 70:1775–1784.

Woolnough DA, Downing JA, Newton TJ (2009) Fish movement and habitat use depends on water body size and shape. Ecol Freshw Fish 18:83–91. doi: 10.1111/j.1600-0633.2008.00326.x

Yates C a, Erban R, Escudero C, et al (2009) Inherent noise can facilitate coherence in collective swarm motion. Proc Natl Acad Sci U S A 106:5464–5469. doi: 10.1073/pnas.0811195106

Zhao M, Heinsch FA, Nemani RR, Running SW (2005) Improvements of the MODIS terrestrial gross and net primary production global data set. Remote Sens Environ 95:164–176. doi: DOI: 10.1016/j.rse.2004.12.011

Zimmerman CE (2005) Relationship of otolith strontium-to-calcium ratios and salinity: experimental validation for juvenile salmonids. Can J Fish Aquat Sci 62:88–97. doi: 10.1139/F04-182

Zimmerman CZ, Reeves GH (2002) Identification of Steelhead and Resident Rainbow Trout Progeny in the Deschutes River, Oregon, Revealed with Otolith Microchemistry. Trans Am Fish Soc 131:986–993.

Zimmerman JL (1965) Bioenergetics of the Dickcissel, Spiza americana. Physiol Zool 38:127–136.