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Freshwater fish introductions in mediterranean-climate regions: are there commonalities in the conservation problem?

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ABSTRACT

Aim To compare patterns and drivers of freshwater fish introductions across five climatically similar regions and evaluate similarities and differences in the non-native species introduced.

Location Five mediterranean-climate regions: California (USA), central Chile, south-western Australia, the Iberian peninsula (Spain and Portugal) and the south-western Cape (South Africa).

Methods Species presence–absence for native and non-native fishes were collated across the regions, and patterns of faunal change were examined using univariate and multivariate statistical approaches. Taxonomic patterns in freshwater fish introductions were evaluated by comparing the number of species introduced by order to the numbers expected from binomial probabilities. Factors influencing multiple introductions of freshwater fish species in mediterranean regions were determined using generalized linear modelling.

Results High levels of endemism (70–90%) were revealed for south-western Cape, south-western Australia and Chile. Despite their high rates of endemism, all regions currently have more non-native species than endemic species. Taxonomic selection was found for five orders, although this was only significant for Salmoniformes across regions. The average increase in regional compositional similarity of fish faunas resulting from non-native fish introductions was 8.0%. Important factors predicting multiple introductions of a species include previous introduction success and mean latitude of its distribution

Main conclusions The mediterranean-climate regions of the world, separated by vast distances, originally had a few fish species in common but are now more similar, owing to species introductions, illustrating the extent and importance of taxonomic homogenization. Introductions are largely driven by taxonomically biased human interests in recreational fisheries, aquaculture and ornamental pet species.

Keywords

Biological invasions, conservation, freshwater fish, mediterranean-climate regions, taxonomic homogenization, taxonomic selection.

INTRODUCTION

Freshwater ecosystems are subjected to the full range of anthropogenic threats, including habitat loss and fragmentation, hydrological alteration, climate change, overexploitation,

pollution and the global introduction of non-native species (Dudgeon *et al.*, 2006). Consequently, freshwater organisms are among the most imperilled taxa world-wide (Jenkins, 2003). This is well illustrated by the fact that, according to the International Union for Conservation of Nature (IUCN), 25%

of evaluated freshwater fish species are considered threatened with global extinction (Hinton-Taylor *et al.*, 2009). Among the most important factors responsible for these levels of imperilment is the introduction and spread of invasive non-native fishes (Leprieur *et al.*, 2009).

Understanding the multi-faceted process of aquatic invasions is important for the management and conservation of freshwater ecosystems. Within the invasion process, it is during the initial introduction and dispersal stages that management efforts can prevent the establishment and the subsequent impacts of non-native species (Vander Zanden & Olden, 2008). Although a small proportion of non-native species may have neutral or even facilitative effects on native biota and ecosystems (Cope & Winterbourn, 2004; Johnson *et al.*, 2009b), others become invasive, establishing spreading populations and impacting the receiving environment (Mack *et al.*, 2000). Once established, management options for the non-native species are reduced to eradicating or controlling the spread of established populations. Eradication of non-native species can be costly and is rarely accomplished with the exception on small islands, in isolated areas (such as ponds or small headwater ecosystems), or before species have spread widely (Myers *et al.*, 2000; Zavaleta *et al.*, 2001). The eradication may also be opposed by groups benefiting from the presence of the non-native species and the general public (Beamesderfer, 2000), e.g. trout-stocking societies or government-sanctioned fisheries. Thus, preventing unauthorized introductions by targeting the initial dispersal stage is the most effective management option for non-native species (Kolar & Lodge, 2001; Vander Zanden & Olden, 2008).

The introduction of freshwater fishes to new regions is a result of human activities: both intentional (e.g. aquaculture, aquarium release, as live bait, establishing a fishery or bio-control) and unintentional (e.g. inter-basin transfer schemes, ballast water) (Rahel, 2007). Non-native freshwater fishes also have establishment rates that are higher than many other taxa (Jeschke & Strayer, 2006). As a result, 26% of the 1055 catchments evaluated by Leprieur *et al.* (2008a) contained freshwater fish assemblages comprised of between 25% and 95% non-native species, while a further 23% contained between 5% and 25% non-native species. The success of introduced fishes in the establishment phase is perceived to be related to intrinsic ecological and life history characteristics of the species (e.g. reproduction guild, fecundity, dietary breadth and/or environmental tolerances) and extrinsic features of the environment, which are difficult to predict (Marchetti *et al.*, 2004a; García-Berthou, 2007).

As with plants and birds (Lockwood, 1999; McKinney & Lockwood, 1999), phylogenetic history and human affiliation have been identified as predictors favouring introduction of freshwater fish species during the initial dispersal phase (Alcaraz *et al.*, 2005). Certain families and taxa have more non-native species (Clavero & García-Berthou, 2006) because of strong human biases towards introducing species such as game fish, forage fish and bio-control of aquatic weeds or mosquitoes (Kolar & Lodge, 2002; Ruesink, 2003, 2005;

García-Berthou, 2007; Rahel, 2007). Aquaculture has been identified as the major reason for introducing fish species into different countries, with 50% of freshwater fish introduced for aquaculture having established in the wild (Casal, 2006). Further, once a species has been introduced to a catchment, it is likely to be introduced over time to neighbouring catchments in the region (e.g., Alcaraz *et al.*, 2005; Vander Zanden & Olden, 2008).

Large-scale comparative investigations provide a unique opportunity to explore questions related to the patterns and drivers of the present-day biogeography of freshwater fishes (Leprieur *et al.*, 2008a; Blanchet *et al.*, 2009). A comparison of introductions across climatically similar regions promotes an understanding of invasion processes by isolating large-scale drivers other than regional climate (Pauchard *et al.*, 2004) and focuses on the role of human activities (Jiménez *et al.*, 2008) and the characteristics of the invading species (Moyle & Marchetti, 2006). Comparative studies may also provide valuable information for the conservation of native species and the management of non-native species by establishing priority lists of potentially harmful species, evaluating the risk of homogenization of the invaded communities, developing guidelines for sustainable ecosystem management and targeting dispersal pathways for the management of non-native species (Pauchard *et al.*, 2004).

This study aims to compare patterns of freshwater fish introductions across five climatically similar regions to determine commonalities in the taxonomic selection and geographical origin of non-native fishes. We ask whether species introductions have led to a convergence in regional species faunas (taxonomic homogenization) and explore whether specific characteristics of these fish species predisposed them to be introduced to more than one region. Mediterranean-climatic regions have been selected for this study as they are recognized to be centres of endemism and/or high biodiversity (Cowling *et al.*, 1996). In addition, all mediterranean-climate regions are included in the six global freshwater fish invasion hotspots where non-native fishes comprise more than 25% of the fish assemblage (Leprieur *et al.*, 2008a). Lastly, aquatic faunas in mediterranean-climate regions are declining faster than those in any other biome, as a result of a suite of forces including habitat degradation, the impact of non-native species and direct competition with humans for limited water resources (Moyle, 1995; Cuttelod *et al.*, 2009).

METHODS

Study region

We examined five mediterranean-climate regions: California, the Iberian Peninsula (Mediterranean Basin), central Chile, south-western Australia and the south-western Cape of South Africa (Fig. 1). Study areas according to the freshwater ecoregions delineated by Abell *et al.* (2008) include sections of the Oregon and Northern California Coastal and Sacramento-San Joaquin ecoregions (California), the South Andean

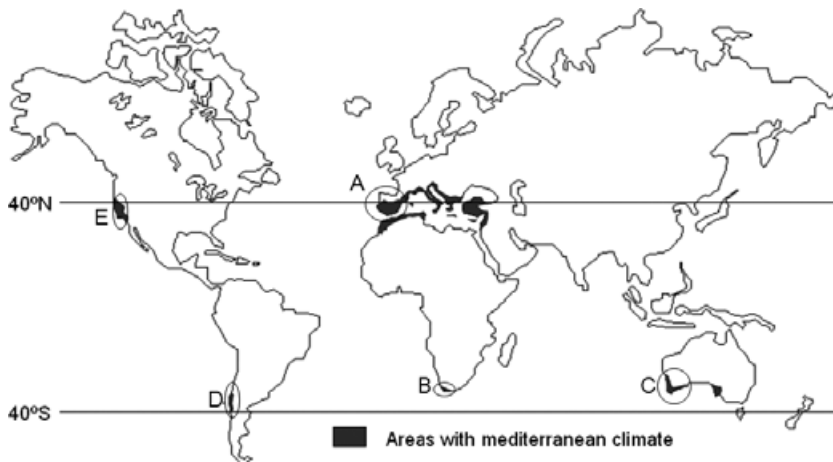


Figure 1 Locations of mediterranean-climate regions examined in this study. Regions included in this study are: the Iberian Peninsula (A), the south-western Cape in South Africa (B), south-western Australia (C), central Chile (D) and California in the USA (E).

Pacific Slope ecoregion (Chile), the Eastern, Southern and Western Iberian ecoregions (Iberian Peninsula), the South-Western Australian ecoregion and the Cape Fold ecoregion (south-western Cape of South Africa).

Data description

Our study focused on bony fish (Class Osteichthyes) that reproduce in fresh water. Only species that have established self-sustaining populations in the region were considered. The ‘historical’ species pools for each region were reconstructed from literature documenting native freshwater fish assemblages, while the ‘present’ species pools were based on the latest surveys for the regions (*c.* 2002), taking into account documented introductions and extinctions. Data of historical and present fish distributions were obtained from the following sources: Moyle (2002) for California, Clavero & García-Berthou (2006) for the Iberian Peninsula, Campos *et al.* (1998), Dyer (2000), Iriarte *et al.* (2005) and Habit *et al.* (2006) for Chile, Morgan *et al.* (1998, 2004, 2006) for south-western Australia and Skelton (2001) for the south-western Cape. A taxonomic revision of the freshwater fishes of the south-western Cape is currently in progress. In this study, the species list for the south-western Cape was restricted to species described in Skelton (2001). The database created comprised of regional scale presence–absence records.

Statistical analysis

Evaluation change in compositional similarity

Jaccard’s index of similarity (Jaccard, 1900) was selected for this work because it is the most commonly used index in previous studies of biotic homogenization (Olden & Rooney, 2006). Compositional similarity (CS) for the historical assemblages ($CS_{\text{Historical}}$) and present-day assemblages (CS_{Present}) was calculated separately for each pair of regions using the PRIMER-E 6.1.5 statistical software package (Clarke & Warwick, 2001). Non-metric multi-dimensional scaling (NMDS) was performed to summarize multivariate patterns in fish

community composition among the regions. NMDS is an ordination method that preserves the rank-ordered distances between sample points in ordination space and for our purposes provided a useful approach for visualizing changes in faunal similarity over time. NMDS uses an iterative approach that rearranges samples in the ordination space to minimize a measure of disagreement (referred to as stress) between the compositional dissimilarities and the distance between the points. In two-dimensional NMDS ordinations, stress values <0.1 correspond to a good ordination with no real prospect of a misleading interpretation (Clarke & Warwick, 2001).

Taxonomic patterns of non-native species

Taxonomic patterns of non-native fish species were evaluated at the order level by comparing the number of species introduced to each region from each order with that calculated assuming random species selection from the available species pool following Alcaraz *et al.* (2005). The global number of freshwater species in each order was obtained from Nelson (2006). The total number of species introduced to each mediterranean region from each order was compared to the expected value using a binomial distribution, based on a random sample of the global species pool. The probability of observing the number of non-native species given the proportion of species introduced in the region and the number of extant species in the order is presented as a *R* value (Lockwood, 1999). We corrected these *R* values with the procedure of Benjamini & Hochberg (1995), as implemented in the *R* package (R Development Core Team, 2008). This procedure controls the false discovery rate (i.e. the proportion of erroneously rejected null hypotheses), balances type I and type II errors and confers several advantages (e.g. more statistical power and adaptation to the ‘amount of signal’ in the data) over more conventional procedures such as the Bonferroni correction (Garcia, 2004).

Variations in the geographical origin of non-native species were determined by allocating the native range of the non-native species to one of 12 regions: Africa, Eastern Asia, Central

Eurasia, Northern Europe, Mediterranean Basin, Circumpolar, North Atlantic, North Pacific, eastern North America, Polar North America, western North America and South America. We tested the independence of regions of origin and introduction with a chi-square test of independence (Sokal & Rohlf, 1995), with a Monte Carlo simulation using SPSS 17 (SPSS Inc., 2008).

Correlates of species establishment

We identified variables to predict the number of mediterranean-climate regions to which a species would be introduced using Generalized Linear Models (GLM) with Poisson distribution. A response variable using the number of regions in which a species had established was defined. Seven of the predictors used (adult trophic status, size of native range, parental care, maximum adult size, maximum adult fecundity, physiological tolerance and previous invasion success: see Table S2 in the supplemental material for explanation) were based on analyses by Marchetti *et al.* (2004c) and Ribeiro *et al.* (2008), and much of the data were sourced from these publications. For species not included in the above publications, the relevant data were obtained from FishBase 2004 (Froese & Pauly, 2004). The scalar variable 'previous introduction success' (the number of countries to which a species has been successfully introduced) was transformed ($\ln(x + 1)$) prior to analysis. Human use and latitude variables (mean latitude, latitude range and aquaculture, aquarium and game fish importance) were derived from FishBase 2004. The mean latitude is included as a surrogate for net primary productivity, a measure of the energy availability that has been demonstrated to be an important predictor of riverine fish species richness patterns globally (Oberdorff *et al.*, 1995; Guégan *et al.*, 1998). The latitude range is included as an additional measure of physiological tolerance of the introduced species. Kendall's tau-b correlation coefficients were used prior to the GLM analysis to assess the correlation between the selected variables (Dytham, 2006) using SPSS 17 (SPSS Inc., 2008). A level of 0.70 was chosen as a maximum for the correlation coefficient (r) following Ribeiro *et al.* (2008). Variables with correlation coefficients greater than the maximum value were excluded from the analysis.

We used Akaike information criteria (AIC) to identify the most plausible GLM models. AIC is a measure based on information theory and maximum likelihood that considers the number of predictors (parsimony) in addition to goodness-of-fit and is used to compare candidate models describing the same data, with the best fitting model having the lowest AIC (Burnham & Anderson, 2002, 2004). We used two procedures in the R software environment (R Development Core Team, 2008) based on AIC to evaluate models: the stepAIC function, which is a stepwise procedure based on the AIC statistic that selects a single model, and a more formal multi-model inference approach (Burnham & Anderson, 2002, 2004) with the MuMIn package (Barton, 2009). In the multi-model inference approach, we computed the models that sum

more than 95% of Akaike weights and computed the relative variable importance (Burnham & Anderson, 2002, 2004), which is the sum of the weights for the variables that are included in any of those models.

RESULTS

Among the mediterranean regions studied, native fish species richness was highest for California (45 species) followed by the Iberian Peninsula (36 species), Chile (25 species), the south-western Cape (18 species) and south-western Australia (10 species) (Fig. 2). The proportion of endemic species historically occurring in each region was highest for the south-western Cape (89%), followed by south-western Australia (80%), California (60%), Chile (52%) and the Iberian Peninsula (44%). Strikingly, the number of non-native species exceeded the number of endemic species for all five regions: California (44 species); Iberian Peninsula (23 species); Chile (18 species); south-western Cape (17 species); and south-western Australia (10 species) (Fig. 2). California is the only region with known species extinctions (*Oncorhynchus gorbuscha* (Walbaum 1792), *Gila crassicauda* (Baird & Girard 1854) and *Pogonichthys ciscoideus* Hopkirk 1974), of which the latter two are globally extinct.

Regional level biotic homogenization

The historical CS among native freshwater fish faunas of the five mediterranean-climate regions, calculated as the average of the pairwise similarities, was zero for nine of the 10 pairwise comparisons, indicating that no species was shared between these regions. South-western Australia and Chile historically shared *Galaxias maculatus* (Jenyns 1842), resulting in a 2.9% historical CS between these two regions. Comparisons of historical versus present fish faunas demonstrated that the mediterranean regions have homogenized over recent time, with the mean CS increasing between 7.2% and 8.6% (mean 8.0%, Table 1). NMDS showed a strong overall tendency towards more similar fish faunas (Fig. 3). Chile showed the

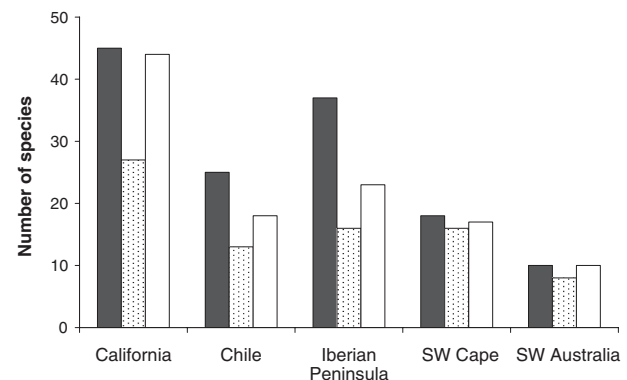


Figure 2 Number of freshwater fish species native (solid bars), endemic (stippled bars) and successfully introduced (open bars) to five mediterranean regions.

Table 1 Summary statistics for the five mediterranean-climate regions. Reported values include the number of native (N), extinct (X) and introduced (I) freshwater fish species, the pairwise compositional similarity between the historical and present-day fish faunas (CS), average change in pairwise composition similarity between historical and present-day fish faunas (ΔCS_{av}) and the pairwise change in composition similarity between regions based on Jaccard's index.

	No. Species					Change in compositional similarity (ΔCS)				
	N	X	I	CS	ΔCS_{av}	California	Chile	Iberian Peninsula	SW Australia	SW Cape
California	45	3	44	47.2	7.2					
Chile	25	0	21	58.1	8.4	8.3				
Iberian Peninsula	36	0	23	61.7	8.6	7.4	10.8			
SW Australia	10	0	10	50.0	7.5	3.9	7.5	8.2		
SW Cape	18	0	17	52.9	8.6	9.1	6.9	8.1	10.2	

greatest change in pairwise CS with the Iberian Peninsula (10.8%; Table 1), while the change in pairwise CS between south-western Australia and the south-western Cape was 10.2%. The smallest change in pairwise CS was between California and south-western Australia (3.9%; Table 1). Although present-day faunal assemblages are more similar to their historical assemblages than to those of any other region, it is apparent that regions have become considerably more similar in present times.

Two species – *Carassius auratus* (Linnaeus 1758) and *Cyprinus carpio* Linnaeus 1758 - have been introduced to all five mediterranean-climate regions, and two species - *Salmo trutta* Linnaeus 1758 and *Oncorhynchus mykiss* (Walbaum 1792) – are native (but not endemic) to the Iberian Peninsula and California, respectively, and have been introduced into each of the other four regions. A further six species - *Ameiurus melas* (Rafinesque 1820), *Gambusia holbrooki* Girard 1859, *Ictalurus punctatus* (Rafinesque 1818), *Micropterus salmoides* (Lacepède 1802), *Perca fluviatilis* Linnaeus 1758 and *Salvelinus fontinalis* (Mitchill 1814) - that are not native to any mediterranean-climate region have been introduced to three regions. Twenty-one species from the families Cyprinidae (3 spp.), Cyprinodontidae (2), Salmonidae (4), Centrarchidae (5), Siluridae (3), Percidae (1) and Cichlidae (3) have been introduced to two or more regions. Two additional species native to California - *Acipenser transmontanus* Richardson 1836 and *Oncorhynchus tshawytscha* (Walbaum 1792) – have been introduced to Chile.

Taxonomic selection

A total of 76 species was recorded as introduced to the five mediterranean regions (see supplemental material: Table S1), 69 of which are from five orders (Cypriniformes (16), Cyprinodontiformes (10), Perciformes (26), Salmoniformes (9) and Siluriformes (8)) (Fig. 4). Eleven orders of freshwater fish have been introduced into one or more of the five mediterranean-climate regions (Table 2). Four orders (Cypriniformes, Cyprinodontiformes, Perciformes and Salmoniformes) have been introduced to all five regions, while Siluriformes have been

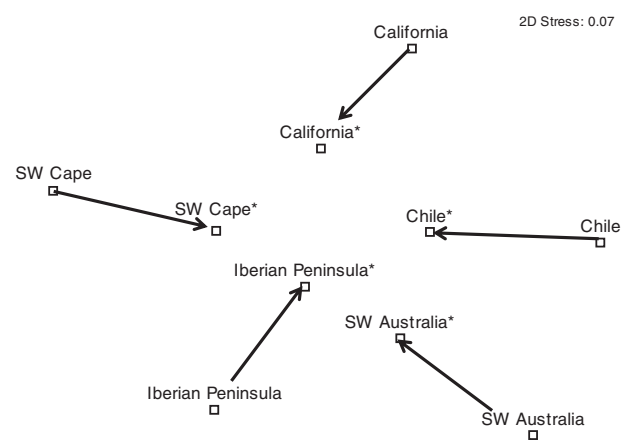
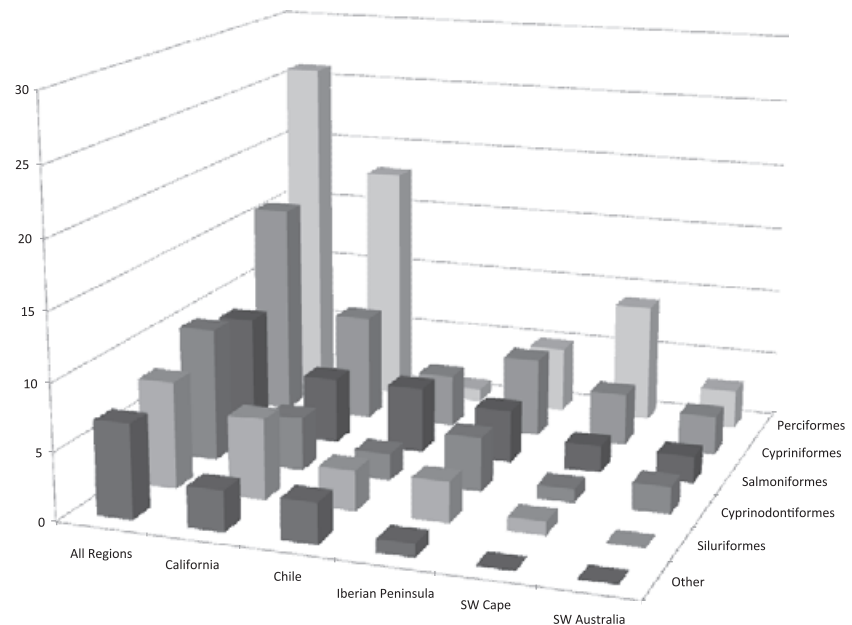


Figure 3 Multidimensional Scaling summarising changes in regional fish composition between historical and present-day (*) time periods. Convergence of regions into the same multivariate space provides evidence for taxonomic homogenization over time.

introduced to all regions except south-western Australia. Salmoniformes are over-represented among non-native species in all five regions (Table 2) ($P < 0.005$), while Perciformes are over-represented in California ($P < 0.005$), the south-western Cape ($P < 0.05$) and when all regions are considered together ($P < 0.05$). Characiformes and Siluriformes were under-represented when all regions are considered together ($P < 0.005$ for Characiformes and $P < 0.05$ for Siluriformes). The set of taxonomic orders introduced to each region was non-random and did not vary significantly between regions ($\chi^2 = 41.2$, Monte Carlo $P = 0.437$).

Species successfully introduced to the mediterranean regions were mostly from eastern North America, with 32 of the 76 species originating from this region (Fig. 5) although most of these were introduced to California. Each region was found to have received species from a diverse set of geographical origins, unique to each region and varying significantly among regions ($\chi^2 = 109.3$, Monte Carlo $P < 0.0005$). No species native to the south-western Cape, south-western Australia or Chile has been successfully introduced to the other regions. No species

Figure 4 Number of freshwater fish introductions to the five mediterranean-climate regions (California, central Chile, the Iberian Peninsula, the south-western Cape, and south-western Australia) by taxonomic order. 'Other' includes Acipenseriformes, Atheriniformes, Characiformes, Clupeiformes, Esociformes and Gasterosteiformes.



endemic to any of the study regions has been successfully introduced to the other regions considered.

Correlates of species establishment in mediterranean-climate regions

The two AIC procedures used produced similar results and suggested that the most plausible predictors of the numbers of regions where a species was introduced were previous introduction success and mean latitude, the former predictor being highly significant and the latter indicative of net primary productivity (Tables 3 and 4). The model selected by the stepwise procedure accounted for 74% of the variation (McFadden R^2), implying that the model describes the data well (Table 3). The rest of variables are less likely to predict number of regions a species would be introduced to. Although many models were plausible according to AIC weights, the best 20 models all included previous introduction success and 9 of the 10 best models included mean latitude.

DISCUSSION

The freshwater fish assemblages of all five mediterranean-climate regions have undergone profound changes. The introduction of species has resulted in the reduction in the characteristic endemism of the regions and has increased the number of species by an average of 80% (64% in the Iberian Peninsula to 91% in California). The highest number of introduced species was found for California, almost double the number of species introduced to any other region. A similar result was found for plants in California and central Chile (Jiménez *et al.*, 2008). Perhaps the most striking finding is that the number of freshwater fish species successfully introduced into each of the mediterranean-climate regions in this study exceeds the original numbers of endemic species, despite the

known high rates of fish endemism in each region. Many of the endemic species of south-western Australia and the south-western Cape are unable to co-exist with the non-native species and have been reduced to relict populations in habitats isolated by barriers to non-native species invasion (Morgan *et al.*, 2002, 2004; Skelton, 2002; Tweddle *et al.*, 2009).

Our results thus show strong evidence of ongoing taxonomic homogenization in the fish faunas of the five mediterranean regions included in this study. The level of homogenization was similar (about 8%) and appears to be independent of the number of species historically native to the area (California has four times the number of native species of south-western Australia). One shortcoming of our regional scale analysis is the difficulty of including translocated species, which have been identified as important in homogenization studies (Leprieur *et al.*, 2008b).

Our results demonstrate that the majority of non-native species in mediterranean-climate regions come from five taxonomic orders (Cypriniformes, Cyprinodontiformes, Perciformes, Salmoniformes and Siluriformes), as noted in previous studies from California (Moyle & Marchetti, 2006), the Iberian Peninsula (Alcaraz *et al.*, 2005) and south-western Australia (Morgan *et al.*, 2004). More than 90% of all introductions (69 of 76) were from these orders, confirming the role of phylogenetic preference and human association in freshwater fish introductions. Salmoniformes, important recreational angling and aquaculture species, were significantly over-represented in all the regions included, a result consistent with a previous study from the Iberian Peninsula (Alcaraz *et al.*, 2005). Perciformes, important recreational angling species, were over-represented in California, the south-western Cape and when all regions were considered together. Characiformes and Siluriformes were under-represented when all regions were considered together, but not in any specific region. Interestingly, Siluriformes and

Table 2 The number of non-native and native freshwater fish species by taxonomic order compared to the total number of freshwater species (Nelson, 2006) in the mediterranean-climate regions. *R* values are the binomial probabilities of taxonomic selectivity of introduced species, comparing the introduced species with the global pool of freshwater fishes. *P* values are the *R* values adjusted for multiple comparisons by the procedure of Benjamini & Hochberg (1995). Significant results ($P \leq 0.05$) are highlighted in bold.

(a) Combined results for all mediterranean-climate regions included in the study					
Order	Global Species	Number of Introduced Species	Number of Expected Species	<i>R</i>	<i>P</i>
Acipenseriformes	14	1	0.1	0.0966	0.1395
Atheriniformes	146	1	1.1	0.3669	0.4336
Characiformes	1343	1	10.2	0.0004	0.0026
Clupeiformes	72	2	0.6	0.0870	0.1395
Cypriniformes	2662	16	20.3	0.0607	0.1315
Cyprinodontiformes	794	10	6.1	0.0427	0.1110
Esociformes	10	1	0.1	0.0712	0.1322
Gasterosteiformes	19	1	0.1	0.1262	0.1641
Osmeriformes	42	0	0.3	0.7250	0.7250
Perciformes	1922	26	14.6	0.0022	0.0095
Salmoniformes	45	9	0.3	<0.0005	<0.0005
Scorpaeniformes	52	0	0.4	0.6716	0.7250
Siluriformes	2280	8	17.4	0.0057	0.0185

(b) California					
Order	Number of native species	Number of species introduced	Number of species expected	<i>R</i>	<i>P</i>
Acipenseriformes	2	0	0.1	0.9364	0.9364
Clupeiformes	0	2	0.3	0.0403	0.1004
Cypriniformes	19	8	11.8	0.0558	0.1004
Cyprinodontiformes	1	4	3.5	0.1938	0.2492
Gasterosteiformes	1	1	0.1	0.0817	0.1226
Perciformes	3	18	8.5	0.0028	0.0127
Salmoniformes	10	5	0.2	<0.0005	<0.0005
Scorpaeniformes	9	0	0.2	0.7835	0.8815
Siluriformes	0	6	10.1	0.0474	0.1004

(c) Iberian Peninsula					
Order	Number of native species	Number of species introduced	Number of species expected	<i>R</i>	<i>P</i>
Cypriniformes	29	6	6.1	0.1605	0.2341
Cyprinodontiformes	3	4	1.8	0.0927	0.1947
Esociformes	0	1	0.0	0.0249	0.0998
Gasterosteiformes	1	0	0.0	0.9526	0.9526
Perciformes	1	5	4.4	0.1755	0.2341
Salmoniformes	1	4	0.1	<0.0005	<0.0005
Scorpaeniformes	1	0	0.1	0.8755	0.9526
Siluriformes	0	3	5.2	0.0974	0.1947

(d) South-western Cape					
Order	Number of native species	Number of species introduced	Number of species expected	<i>R</i>	<i>P</i>
Cypriniformes	14	4	4.5	0.1890	0.2835
Cyprinodontiformes	0	1	1.4	0.3498	0.4198
Osmeriformes	1	0	0.1	0.9308	0.9308
Perciformes	1	9	3.3	0.0045	0.0135
Salmoniformes	0	2	0.1	0.0027	0.0010
Siluriformes	2	1	3.9	0.0794	0.1588

Table 2 (Continued)

(e) South-western Australia					
Order	Number of native species	Number of species introduced	Number of species expected	R	P
Cypriniformes	0	3	2.7	0.2194	0.2638
Cyprinodontiformes	0	2	0.8	0.1431	0.2607
Osmeriformes	6	0	0.0	0.9587	0.9587
Perciformes	3	3	1.9	0.1739	0.2609
Salmoniformes	0	2	0.1	0.0010	0.0060
Siluriformes	1	0	2.3	0.1014	0.1599

(f) Chile					
Order	Number of native species	Number of species introduced	Number of species expected	R	P
Acipenseriformes	0	1	0.0	0.0247	0.1112
Atheriniformes	5	1	0.3	0.2024	0.2757
Characiformes	2	1	2.4	0.2144	0.2757
Cypriniformes	0	4	4.8	0.1819	0.2757
Cyprinodontiformes	0	2	1.4	0.2453	0.2760
Osmeriformes	7	0	0.1	0.9269	0.9269
Perciformes	4	1	3.5	0.1077	0.2757
Salmoniformes	0	5	0.1	<0.0005	<0.0005
Siluriformes	7	3	4.1	0.1895	0.2757

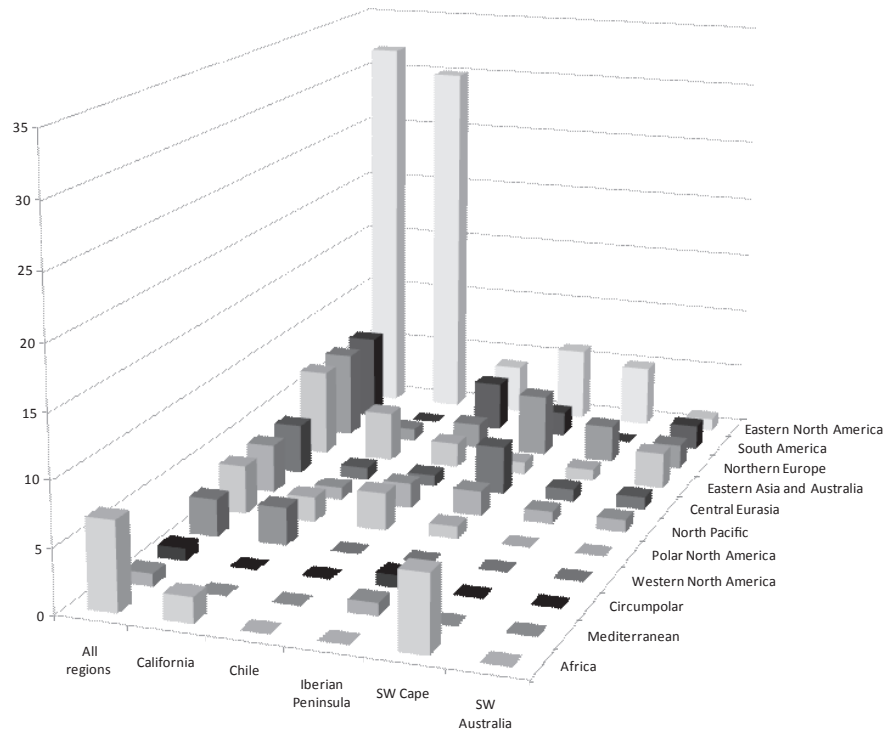


Figure 5 Number of freshwater fish species introduced to the five mediterranean-climate regions (California, the Iberian Peninsula, central Chile, the south-western Cape, and south-western Australia) by geographic origin.

Characiformes are orders that have large numbers of tropical species that may not be able to establish in mediterranean-climate regions, where the temperature ranges and harsh abiotic conditions may extend beyond their physiological tolerance. Cypriniformes is a large order that has not been introduced to the same extent as smaller families, such as

Salmonidae, perhaps because of the lack of value placed on members of this order by recreational angling and the aquaculture industry.

The geographical origins of the species introduced to the five mediterranean regions show some interesting patterns. Each region received species from a unique set of geographical

Table 3 Generalized linear model (Poisson distribution) predicting the number of mediterranean-climate regions where a species successfully established, selected by the stepwise algorithm and the Akaike Information Criterion.

	Coefficient	SE	z value	P value
Previous introduction success	0.373	0.074	25.463	<0.0005
Mean latitude	0.902	0.504	3.199	0.074
Constant (intercept)	-1.060	0.414	6.557	0.010

Table 4 Relative importance of variables (sum of the Akaike weights for the variables included in the models that added 95% of the Akaike weights) in the Generalized linear models (Poisson distribution) predicting the number of mediterranean-climate regions where a species was introduced.

Variable	Relative variable importance
Previous introduction success	1.00
Mean latitude	0.58
Importance as a game fish species	0.28
Importance as an aquarium species	0.26
Physiological tolerance	0.24
Importance as an aquaculture species	0.24
Size of native range	0.24
Maximum adult length	0.23
Latitude range	0.23
Adult fecundity	0.23
Adult fecundity	0.23
Adult trophic status	0.01

origins. The diversity of geographical origins poses a challenge to conservation authorities, because the diversity of origins makes it difficult to identify potential source regions of species that would successfully establish. A similar result was obtained for plants in central Chile and California (Jiménez *et al.*, 2008). This highlights the importance of studies aimed at identifying characteristics of species that have successfully established self-sustaining populations in other mediterranean-climate regions. Eastern North America was an important source of introductions to most regions, but particularly to California (30 of 32 species introduced to California, while 11 species introduced to the other regions). Similarly, the south-western Cape contains the highest number of the species of African origin (five of six), while only two African species have established in California. One eastern Australian species [*Bidyanus bidyanus* (Mitchell 1838)] has established in south-western Australia (see Morgan *et al.*, 2004), probably an escapee from aquaculture. Comparable effects of geographical proximity are seen for the Iberian Peninsula with European and central Eurasian species and for central Chile, with South American species. These cases could be viewed as regional translocations.

Many bird and plant families with a significantly high concentration of non-native species have traits that encourage

purposeful human transport [e.g. birds for sport (pheasants, Phasianidae), pets (parrots, Psittacidae) and plants as ornamentals (roses, Rosaceae)] (McKinney & Lockwood, 1999; Blackburn *et al.*, 2009). Jiménez *et al.* (2008) found higher naturalized species diversity for California; differences in the proportion of species according to geographical origin; differences in the proportion of species according to taxonomic composition of their non-native flora; and a trend towards higher similarity between the non-native floras of latitudinal bands associated with higher levels of human disturbances in their comparison of introduced flora in California and central Chile. This study confirmed similar patterns in freshwater fish introductions for the first two findings. We did not find significant differences in taxonomic orders introduced to the regions and found homogenization of about 8% as opposed to the differentiation found for plants. Because of the nature of our study, it was not possible to evaluate Jiménez *et al.*'s fourth finding. In evaluating the establishment success of birds in mediterranean-climate regions, Kark & Sol (2004) found that six families accounted for more than 78% of introductions and that species and families were non-randomly introduced to the respective regions. For freshwater fishes, six families accounted for 74% of the species established in mediterranean-climate regions, and the taxonomic orders introduced were non-randomly introduced to the respective regions.

Spatial scale is an important consideration when studying biotic homogenization (Olden, 2006). Olden (2006) argues that levels of homogenization would be greater grains of investigation than at smaller grains. This is supported by a few studies. Fish fauna homogenization was greater at coarser spatial scales (Californian zoogeographical provinces, Canadian provinces and Australian drainage divisions) than for smaller scales (catchments, or ecoregions, within these provinces/drainage divisions) (Marchetti *et al.*, 2001, 2006; Taylor, 2004; Olden *et al.*, 2008). Similarly, the appropriate choice of observation unit is closely associated with spatial scale (Olden, 2006). Analyses based on political units are likely to underestimate biotic homogenization because historical similarity will be higher because natural, biogeographical barriers defining historical distinctiveness of a region are violated (Olden, 2006). The most appropriate scale for freshwater fish studies may therefore be the catchment.

Our results demonstrated that previous introduction success and mean latitude, an estimate of net primary productivity, were the most important predictors of whether a species would be widely introduced in mediterranean-climate regions. The results of this study are not completely comparable to previous studies, because the question asked in this study was 'Which characteristics determine why a species is widely introduced in mediterranean-climate regions?', while previous studies have asked 'Which characteristics of a species determine introduction success?'. Thus, it is difficult to compare the results of this study to previous studies (Kolar & Lodge, 2002; Ruesink, 2003; Marchetti *et al.*, 2004b,c; Ruesink, 2005; Moyle & Marchetti, 2006; García-Berthou, 2007; Ribeiro *et al.*, 2008). García-Berthou (2007) found that taxonomic selection, human

affiliation and fish size were important predictors favouring introduction, the taxonomic bias favouring game fish, forage fish and bio-control agents. The perception that the non-native species would occupy an ecological niche unoccupied by the native community (Moyle & Marchetti, 2006) may explain why so many game fish (piscivores) have been introduced, especially into the south-western Cape, south-western Australia, central Chile and the Iberian Peninsula, since the native fish assemblages of these areas do not contain piscivorous species suitable for recreational angling. The introduction of salmonids world-wide could also be attributed to European colonization and the spread of species that the colonists were familiar with by acclimation societies (Cambray, 2003a,b; McDowall, 2006; Crawford & Muir, 2008).

IMPLICATIONS FOR CONSERVATION

The native freshwater fish faunas of mediterranean regions are subject to a wide variety of pressures, including water abstraction, habitat degradation (eutrophication, salinization and channelization) and fragmentation, pollution and the presence of non-native fishes (Crivelli, 1995; Crivelli & Maitland, 1995; Moyle, 1995; Morgan *et al.*, 2003). Conservation of these highly endemic assemblages is a paramount challenge for conservation managers, researchers and officials, as the impact of freshwater fish introductions is greatest in regions of high endemism (Ruesink, 2005). Conservation should be a high priority in these regions, and it is therefore important that control strategies for known invasive species be implemented and the introduction, and spread, of 'new', potentially invasive species be prevented. Further, plans for the conservation and restoration of habitat and water quality should be outlined and implemented. We therefore ask whether the conservation issues are the same for each region and what lessons relevant to the conservation of native species have been highlighted by this study.

The freshwater fish introductions in the Iberian Peninsula are currently driven by illegal introductions, predominantly by anglers (Clavero & García-Berthou, 2006). In the south-western Cape, the nature conservation authority enthusiastically spread alien angling species prior to 1980 (Coke, 1988). This resulted in the loss of many populations of native species through direct predation and competition for resources with non-native fishes (Cambray, 2003b). Subsequently, recreational anglers have been the predominant vector for freshwater fish introductions (Cambray, 2003a,b; Impson, 2006). In Chile, the creation of recreational fisheries was the primary reason for fish introductions prior to the 1980s (Basulto, 2003). Government-sponsored aquaculture has been the major driving force for fish introductions since the 1980s (Iriarte *et al.*, 2005). The expansion of aquaculture has resulted in Chile becoming the world's second largest producer of cultured salmonids (Arismendi *et al.*, 2009), accounting for more than 73% of Chile's aquaculture production (Buschmann *et al.*, 2009). Arismendi *et al.* (2009) found that the relative abundance of free-living salmonids is closely related to the level of fish farming

productions, while relative abundance of native fishes is inversely related. In southern Chile, trout (*S. trutta* and *O. mykiss*) account for more than 60% of total fish abundance and more than 80% of total biomass, while 40% of the streams sampled did not have any native fish (Soto *et al.*, 2006). The introductions in south-western Australia were driven primarily by the legal and illegal spread of mosquitofish, aquarium releases, government-sanctioned spread of game fish (*O. mykiss* and *S. trutta*) and the illegal spread of *P. fluviatilis* (Morgan *et al.*, 2002, 2004). In California, the problem is complex and is the result of a combination of forces, including water-transfer schemes, pressure for recreational angling and aquaculture, ballast water (e.g. Shimofuri goby *Tridentiger bifasciatus* Steindachner 1881) and the aquarium industry (Moyle & Marchetti, 2006).

Where should conservation authorities start in addressing freshwater fish introductions to mediterranean-climate regions? Previous introduction success is a good indicator that a species has a higher probability of establishing (Marchetti *et al.*, 2004c; Moyle & Marchetti, 2006; Ribeiro *et al.*, 2008). The success to failure ratio in California for species that have established in 10 or more countries is 4:1, in comparison to a 1:1 ratio for species that have no previous record of successful establishment (Moyle & Marchetti, 2006). A list of species that have been successfully introduced to more than 10 countries could be established and international trade of these species restricted. Unfortunately, it is likely that many of these species are economically profitable aquaculture species, and restricting trade may be challenging.

Our results suggest that knowing the reason for transport (e.g. aquaculture and recreational angling) is useful in determining the number of regions to which they have been introduced. Therefore, it is important to engage with aquaculture practitioners and recreational anglers to establish ways in which the continued introduction of non-native species can be reduced or eliminated. It is important to recognize that vectors for freshwater fish introductions can change over time (Olden *et al.*, 2010), as has been shown for the Laurentian Great Lakes (Ricciardi, 2006). Intentional introductions to establish recreational fisheries are rare today, and greater care is taken to prevent the release of species introduced for aquaculture. The illegal introduction of game fish remains a persistent insidious vector in many regions (Johnson *et al.*, 2009a), while the release of unwanted aquarium species has become the major introduction vector in countries such as Australia (Lintermans, 2004) and the USA (Smith *et al.*, 2008). Further, the effects of climate change on changing the demographics of species successfully introduced to mediterranean-climate regions, and their management, need to be considered (Rahel & Olden, 2008).

Since aquaculture is a commercially driven activity, one possible management scheme could be to engender self-regulation, with the provision that practitioners pay for eradication of new populations of aquaculture species. An alternative could be annual permitting of aquaculture facilities with a penalty of permit revocation should the facility be

implicated in the release of species to natural watercourses. Aquaculture facilities should be inspected regularly and limited to techniques that pose a low risk of release to natural environments. In Chile, as in many countries, government regulatory, monitoring and enforcement efforts are compromised by limited financial and technical resources and a shortage of relevant scientific research (Buschmann *et al.*, 2009). As a result, the private sector has created different forms of self-regulation for salmonid aquaculture. These efforts appear to be modifying the behaviour of the salmon producers, but an open, multidisciplinary and independent science-based assessment of their ability to control the environmental and social impacts of the industry is required (Buschmann *et al.*, 2009). In Europe, a new regulation (Council Regulation 708/2007, of 11 June 2007) establishes the use of non-native and locally absent species in aquaculture.

Recreational angling is more challenging to manage because of the variety of target species involved. As a result, self-regulation is unlikely to prevent further introductions. Illegal stocking is nullifying multi-million dollar native fish recovery projects, damaging sustainable recreational fisheries worth billions of dollars, threatening native species with extinction and diverting conservation resources away from programmes that benefit fishing and aquatic resources and into expensive and often recurring remediation programmes (Johnson *et al.*, 2009a). Angling is a recreational activity, and its governing bodies are unlikely to have the funds to pay for the eradication of new populations. Organized angling contributes to the local economy of rural regions where fishing competitions are held or where fisheries have been established for specific species (e.g. trout farms). Conservation authorities and provincial government could offer financial incentives to landowners to conserve native fish in the natural watercourses on their properties. An alternative approach could be the introduction of annual permits for landowners who gain beneficial use of non-native fishes on their properties. Conservation authorities can, and must, be more effective in preventing illegal fish stocking through strategic education programmes, proactive regulatory policy, universally severe penalties, generous rewards for reporting illegal stocking and inter-jurisdictional collaboration (Johnson *et al.*, 2009a).

This study confirms the findings of Alcaraz *et al.* (2005) and Clavero & García-Berthou (2006), indicating the relationship of phylogenetic affinity and human use in freshwater fish introductions. It should be noted that the introduction of freshwater fish species predominantly occurs as a result of intentional dispersal. The human dimension of freshwater fish conservation can therefore no longer be ignored. Conservation has always been a crisis-driven cross-disciplinary biological science, trying to deal with problems that have a social origin. Education is a vital component of freshwater fish conservation, as the majority of players (riparian landowners, farming communities, anglers, aquaculture installations and hobby aquarists) are unaware of the long-term impact of their activities. The necessary skills to educate the public and participants in freshwater-fish-related activities are available and should be

utilized to engender long-term conservation ethics among interested and affected parties and the general public. Finally, greater scientific rigour is required in developing conservation strategies for freshwater fishes in conjunction with improved conservation planning strategies (Olden *et al.*, 2010).

ACKNOWLEDGEMENTS

We thank Charmaine Uys and anonymous reviewers for their input and comments regarding this study. S.M.M. acknowledges the financial support of the DST/NRF Centre of Excellence for Invasion Biology and the David and Elaine Potter Foundation during his PhD studies. J.D.O. and E.G.B. acknowledge funding support from the USGS Lower Colorado River Aquatic GAP Program and the Spanish Ministry of Science (CGL2009-12877-C02), respectively. D.L.M. acknowledges Dr Stephen Beatty (Murdoch University) for his work on the fishes of south-west Australia.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 List of species introduced to different mediterranean-climate regions describing the family, order and the native range.

Table S2 Variables included in the generalized linear modelling to test for the importance of different factors influencing the number of mediterranean-climate regions where a species have successfully established.

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BIOSKETCH

S.M. Marr completed this manuscript as part of his PhD thesis under the supervision of J.A.D., C.L.G. and P.H.S. His research focuses on the conservation of the endemic freshwater fishes of the Cape Floristic Region, South Africa, and the management of non-native fish species that threaten their survival.

Author contributions: S.M.M. conceived the ideas and coordinated the research team; S.M.M., M.P.M., E.G.B., I.A. and D.L.M. compiled the data; S.M.M. and E.G.B. collated and analysed the data, and S.M.M. led the writing under the guidance of M.P.M. and J.D.O. and the remaining authors. All authors contributed to the manuscript.

Editor: David Richardson