



Conservation biogeography of freshwater fishes: recent progress and future challenges

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ABSTRACT

Aim To identify key research questions and challenges that will, if addressed in a timely manner, significantly advance the field of freshwater fish biogeography and conservation.

Location Globe.

Methods By drawing on expertise from different regions of the world, we integrate an illustrative conspectus of recent scientific advancements in fish biogeography with a prospectus of needed areas of scientific inquiry to identify information gaps and priority research needs to advance the science.

Results We identified the following core challenges: (1) Testing current and forging new theories in biogeography; (2) Advancing a trait-based biogeography of freshwater fishes; (3) Quantifying extinction risk and loss of fish species in a changing environment; (4) Evaluating the magnitude and geography of extinction debt for freshwater fishes; (5) Elucidating the patterns and drivers of freshwater fish invasions; (6) Forecasting the future geography of freshwater fishes; (7) Understanding the interactive effects of multiple stressors in freshwater ecosystems; (8) Quantifying new features of the biodiversity crisis: fish faunal homogenization and the emergence of novel assemblages; (9) Promoting scientific rigour in emerging freshwater fish conservation strategies and (10) Improving conservation planning strategies for freshwater fish species.

Main conclusions By reflecting on recent scientific progress in fish conservation biogeography, we have identified a set of core challenges and priorities requiring future research investment.

Keywords

Biological invasions, climate change, conservation planning, functional diversity, species diversity.

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INTRODUCTION

Early naturalists Alfred Russel Wallace and Charles Darwin inspired famous ideas of change in life, but also revealed the range of life, that is how organisms were distributed across the globe. Historical biogeography tells us that every single taxon exhibits its own distributional pattern and its own unique history. Some species are known from only a single location, whereas others occur high to low, east to west or poles to tropics, and the ecological and evolutionary implications of their distributions are far reaching (Darwin, 1839; Wallace, 1876). Freshwater fishes exemplify this phenomenon well, because high diversity and endemism stem largely from the fact

that fresh waters are embedded within a terrestrial landscape that limits dispersal within and among drainage basins. These factors underlie an interesting observation: at regional to global scales, most freshwater fishes occupy only a fraction of the localities where they might otherwise thrive (Darlington, 1948). This constrained geography is at least partially responsible for the fantastic diversity of freshwater fishes seen around the world (Berra, 2001; Lévêque *et al.*, 2008).

Freshwater ecosystems have distinctive properties that both underpin and challenge many key tenets of conservation biogeography. Conservation biogeography refers to the application of biogeographical principles, theories and analyses to the conservation of biodiversity (Whittaker *et al.*, 2005).

Freshwater organisms, such as fishes, are subject to several biogeographic constraints that are unique to the aquatic realm. Their ability to move in response to environmental change is constrained by the dendritic arrangement of riverine ecosystems, as well as a variety of physiographic barriers (Fausch *et al.*, 2002). At the largest spatial scales, the movements of freshwater fishes are limited by their inability to cross oceans, high mountain ranges or expansive deserts (Myers, 1949; Parenti, 1991). In the absence of human intervention, large-scale range expansions are normally a result of rare events such as river captures, massive floods that produce dispersal corridors and unintentional movement by terrestrial organisms (Banarescu, 1990; Burrige *et al.*, 2006). At smaller spatial scales (i.e. within river basins), freshwater fish distributions are determined by a combination of biotic and abiotic factors (including barriers to dispersal) that vary longitudinally along the river network (Jackson *et al.*, 2001a). This hierarchy of barriers results in river basins forming what can effectively be considered biogeographical islands (Hugueny *et al.*, 2010).

Habitat isolation and dispersal limitation that have generated high freshwater fish diversity also can increase the risk of species extinction. Freshwaters are subjected to a panoply of anthropogenic threats, including habitat loss and fragmentation, hydrologic alteration, climate change, overexploitation, pollution and the spread of invasive species (Dudgeon *et al.*, 2006). For example, humans now appropriate >50% of available freshwater run-off (Jackson *et al.*, 2001a,b), reservoirs trap 25% of the global sediment load before it reaches the oceans (Syvitski *et al.*, 2005), river systems have been fragmented by *c.* 1 million dams globally (Nilsson *et al.*, 2005), and many inland fisheries are vulnerable to collapse (Allan *et al.*, 2005). The end result is that freshwater fishes are among the most imperilled faunas worldwide. For instance, 40 of the known 1061 North American freshwater fish species became extinct during the twentieth century. This extinction rate is 1000 times higher than the estimated background level for freshwater fishes and much higher than extinction rates estimated for most terrestrial and marine systems (Ricciardi & Rasmussen, 1999). Recent global estimates indicate that 25% of evaluated freshwater fish species are considered threatened with extinction (Vié *et al.*, 2009).

Mounting evidence suggests that the dual processes of human-mediated extirpation of native populations and the introduction of non-native species have resulted in significant changes in freshwater fish faunas at regional and global scales. With this in mind, there are two stark realities regarding the future biogeography of freshwater fishes. First, there is no doubt that fish species are being intentionally and accidentally moved around the world at an unprecedented rate, and many now occur in regions they could never have invaded on their own (Copp *et al.*, 2005; Rahel, 2007; Leprieur *et al.*, 2008). Second, human enterprise has greatly accelerated the pace at which native fish populations are reduced or eliminated (Bruton, 1995; Harrison & Stiassny, 1999; Olden *et al.*, 2007). What is not so clear is the effect these changes will have on freshwater fish biogeography in the future, and what

can be performed to minimize or reverse them. To address these questions, ecologists are challenged to reconcile the historical biogeography of native fishes with the rapid advance of non-native species that is now occurring, against a backdrop of ongoing environmental change.

In our synthesis, we put forward 10 research challenges to advance our knowledge of the linkages between natural and human-induced environmental change and patterns of freshwater fish biogeography. By drawing on expertise from different regions of the world, we offer a prospectus on key research questions to address each challenge (Table 1). The challenges and questions discussed below are not intended to be exhaustive but instead are considered representative of under-studied, yet critical conservation research topics. Our approach is to integrate recent advances in freshwater fish biogeography with a review of information gaps and priority research areas.

CHALLENGE 1: TESTING CURRENT AND FORGING NEW THEORIES IN BIOGEOGRAPHY

Freshwater ecosystems present unique opportunities to test the generality of biogeographical patterns and hypotheses (see Introduction). It is therefore surprising that so few biogeographic studies have been performed with freshwater fishes. Below, we discuss three prominent research themes – Tobler's first law of geography, the Unified Neutral Theory of Biodiversity and ecological niche conservatism – that are largely unexplored within the fish literature but have the potential to greatly advance freshwater fish conservation.

Tobler's first law of geography and distance decay of similarity

The biogeography of freshwater fishes is tightly linked to numerous mechanistic factors, such as the capability for dispersal, physiological constraints of climate and interactions with other species. Recent attention has focused on patterns of distance decay in species similarity; a line of inquiry based largely on Tobler's first law of geography which states that 'Everything is related to everything else, but near things are more related than distant things' (Tobler, 1970). Distance decay describes the biogeographic phenomenon that the compositional similarity between localities (or regions) often decreases or decays as the distance between them increases (Nekola & White, 1999). Distance decay is expected not only as a consequence of dispersal limitation (e.g., because of geographic barriers), but also from spatially structured environmental gradients that shape assemblage structure. Distance–decay curves have now been studied across a wide range of organisms and environments (reviewed in Soininen *et al.*, 2007) but remain poorly understood for freshwater ecosystems. However, two recent studies have provided some of the first insight into the importance of this phenomenon for fish conservation. For major river basins in Europe, Leprieur *et al.* (2009) found significant distance–decay relationships in native

Table 1 Key scientific challenges and timely questions to advance the conservation biogeography of freshwater fishes.

Challenge 1: Testing current and forging new theories in biogeography

- Can modern network theory be integrated with distance–decay analyses and used to account for the hierarchical dendritic structure of riverine ecosystems?
- To what extent do contemporary versus historical factors describing environmental factors and dispersal limitation shape present-day distributions of freshwater fishes at regional, continental and global scales?
- To what degree does neutral theory explain patterns in fish abundance and diversity at different spatial and temporal scales, and how can this knowledge be applied to conservation efforts?
- Do freshwater fishes display metacommunity dynamics, and if so, what are the mechanisms (i.e., neutral, mass effect, species sorting or patch dynamics perspectives) shaping these patterns?
- Do freshwater fishes display ecological niche conservatism, and if so, what are the species traits and environmental factors that influence whether a niche is evolutionarily labile or conserved?

Challenge 2: Advancing a trait-based biogeography of freshwater fishes

- Does a trait-based approach provide new insight into patterns and processes of biogeographical variation in fish species distributions, and if so, can this information inform conservation strategies?
- Does the functional composition of freshwater fish communities converge along similar environmental gradients in disparate regions of the world? If so, does this mean that phylogenetically unrelated communities sharing similar environmental histories will respond similarly to future environmental change?
- Can a trait-based approach help resolve the ‘invasion paradox’ that describes empirical support for both a negative and positive relationship between native species richness and the invasion success of non-native fishes?
- Given the potentially large number of candidate biological traits, but lack of trait data for many fish species in particular regions, which subset of traits are most appropriate for defining functional diversity and offer the most promise for predicting responses to environmental change?

Challenge 3: Quantifying extinction risk and loss of fish species in a changing environment

- What biological traits predispose fish species to the primary components of the extinction process (i.e., rarity, risk of local extirpation and vulnerability to global extinction)?
- Can the identification of extinction-prone traits inform conservation strategies at biogeographic scales?
- Under what circumstances do the assumptions of species–discharge relationships hold for freshwater fishes, and how might we improve this approach by incorporating other mechanistic drivers of biodiversity (e.g. habitat variability, energy availability and extinction dynamics) and accounting for the effects of spatial scale?

Challenge 4: Evaluating the magnitude and geography of extinction debt for freshwater fishes

- What is the level of extinction debt for threatened and endangered fish species, and for what life history (traits) strategies and in which regions of the world are these debts the highest?
- What regional-scale ecological management and restoration actions are required to avoid or significantly delay the manifestation of extinction debts?
- What is the magnitude and geography of immigration credit associated with pending fish species invasions, and what are the implications for the conservation of native biodiversity?
- What are the essential components of a standardized long-term monitoring programme aimed at understanding the processes and testing the mechanisms associated with extinction debts of representative at-risk species?

Challenge 5: Elucidating the patterns and drivers of freshwater fish invasions

- How do the magnitude of different vectors and routes of fish introductions vary geographically, and how might these change in the future?
- Given social demands and economic development, what are the most likely time-scales and scenarios of introduction, establishment and spread of non-native fishes within more pristine freshwater ecosystems?
- To what extent does the current geographical bias in our understanding of invasive fish species affect our ability to diagnose and predict impacts of the literally thousands of other invasive species on numerous poorly-studied locations?
- How do interactions between natural and human processes affect the establishment success of introduced species?

Challenge 6: Forecasting the future geography of freshwater fishes

- How will climate change modify fish distributions, which species are most likely to prosper under particular climate change signals and which ecosystems are most at risk?
 - Can our (currently) limited knowledge of freshwater fish ecological requirements, physiological constraints and ecophysiological relationships be generalized to develop simple mechanistic models to forecast ecological responses to environmental change over regional and global scales?
 - Can key processes involved in determining niche breadth, dispersal limitation and bioenergetics be incorporated into species distribution models to provide more robust predictions in a changing environment?
 - How robust are rapidly emerging techniques that seek to better quantify and incorporate uncertainty in predictive modelling of species distributions?
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Table 1 (Continued)

Challenge 7: Understanding the interactive effects of multiple stressors in freshwater ecosystems

- How can researchers incorporate multiple drivers of environmental change into better experimental and modelling studies to quantify their interactive effects on fish assemblages?
- How is future climate change likely to increase or decrease the ecological impacts of invasive fish species?
- Can multiple environmental factors interact in an antagonistic manner, resulting in a lower overall negative effect on native fishes?

Challenge 8: Quantifying new features of the biodiversity crisis: fish faunal homogenization and the emergence of novel assemblages

- What are the ecological consequences of fish faunal homogenization for native fish species at local, regional and global scales?
- What are the temporal dynamics of taxonomic and functional homogenization in poorly studied regions of the world?
- What are the primary environmental and biological drivers of fish faunal homogenization at different spatial and temporal scales?
- How will rates and patterns of biotic homogenization respond to shifting pathways of species introductions and future environmental change?
- What novel fish assemblages are likely to emerge in response to climate change?

Challenge 9: Promoting scientific rigour in emerging freshwater fish conservation strategies

- Is managed relocation a justifiable conservation strategy for freshwater fishes?
- Are there unique rules of engagement for managed relocation in fresh waters? When and where should managed translocation of fish be considered in freshwater systems, and for which species?
- What are the trade-offs between increasing versus decreasing connectivity when seeking to promote native fishes while simultaneously minimizing the spread of non-native species?
- How can we best assess whether managed relocation of a species will have a detrimental impact on the receiving system, particularly if that system will be dramatically different in coming decades?

Challenge 10: Improving conservation planning strategies for freshwater fish species

- How can we best define and incorporate general principles that describe key ecological, evolutionary and sociopolitical processes into systematic conservation planning to conserve fish biogeography into the future?
- What conservation benefits are there from moving beyond species to incorporate community-level surrogates and measures of functional and phylogenetic diversity as targets for conservation planning (e.g. to maintain long-term demographic processes and genetic integrity)?
- How can measures of species-specific directional connectivity be better integrated into systematic conservation planning approaches to maintain freshwater fish biogeography?
- How can classic systematic conservation planning research be better integrated with models predicting shifts in fish species distributions under future environmental change (e.g. by identify and prioritizing dispersal corridors through time)?
- How can uncertainty arising at multiple phases of the conservation planning process be effectively quantified and accounted for in future efforts?

fish fauna similarity between basins – a pattern explained by the presence of major geographical barriers that limit fish dispersal. Shurin *et al.* (2009) compared the distance–decay rate of species turnover for major taxonomic groups in North America and found that in contrast to freshwater invertebrates that display both passive and active movement strategies, fish were subjected to greater dispersal limitation.

Unfortunately, relatively little is known about fish dispersal within river networks (Rodriguez, 2002). This is partially attributed to the fact that ecologists are now just beginning to use robust, ecologically relevant measures of hydrologic connectivity in their studies. In contrast to the myriad of metrics describing terrestrial landscape connectivity, only recently we have witnessed advancements in the aquatic realm in terms of conceptual understanding (Campbell Grant *et al.*, 2007), index development (e.g., Olden *et al.*, 2001; Cote *et al.*, 2009) and appropriate statistical methodologies (Peterson *et al.*, 2007). Through better representation of hydrologic connectivity in freshwater ecosystems, we expect to achieve a better understanding of how opportunities and constraints to dispersal shape patterns of fish diversity locally (α -diversity), among-localities (β -diversity) and regionally (γ -diversity). Moreover, by gaining a more robust quantification of stream network topologies, we will be better positioned to explore

distance–decay relationships (Hitt & Angermeier, 2008). This will assist conservation planning efforts that seek to identify the best functional form of the distance–decay curve, a reflection of how diversity is spatially distributed, which should facilitate the design of protected areas within river networks (Morlon *et al.*, 2008). For instance, detecting a threshold distance from which species similarity remains constant can help identify freshwater fish biogeographical regions and assess the distance at which freshwater protected areas should be separated to maximize protection of distinct fish faunas.

The Unified Neutral Theory of Biodiversity

Traditional thinking in ecology has stressed local interspecific interactions and niche relationships as determinants of assemblage structure, but ecologists recently have begun to give more attention to multiple processes operating over a hierarchy of spatial scales (Ricklefs, 2008). The Unified Neutral Theory of Biodiversity (UNTB) was proposed to explain species diversity and abundance based on the assumption that individuals of trophically similar species are functionally equivalent, and consequently species distributions are affected mainly by the drift resulting from the stochastic processes of births, deaths and speciation (Hubbell, 2001). By contrast, the

niche assembly theory (also discussed in Challenge 2) posits that non-neutral processes describing differences among species in their environmental tolerances, niche requirements and competitive abilities, ultimately determine species coexistence (MacArthur & Levins, 1967). The neutral and the niche assembly theories can be considered two extremes of a continuum (Gravel *et al.*, 2006).

The UNTB has only recently been explored in freshwater ecosystems; in particular for fishes. Muneeppeerakul *et al.* (2008) proposed a neutral model that simultaneously investigated several ecological patterns of fish communities (e.g., species occupancies, the species–area relationship and the distance decay of assemblage similarity) in the Mississippi–Missouri River Basin, United States. Their model emphasized the importance of dispersal in a metacommunity context (Leibold *et al.*, 2004) and was calibrated using the product of basin area and average annual run-off production as an indicator of habitat capacity for each sub-basin. Overall, their process-based model successfully predicted observed patterns of freshwater fish diversity, without detailed knowledge about species interactions. This is perhaps not a surprising result given that their models were calibrated at a coarse spatial grain (i.e., mean basin area = 5000 km²), at which the importance of species interactions is generally overwhelmed by environmental heterogeneity (Jackson *et al.*, 2001a). The neutral model of Muneeppeerakul *et al.* (2008) clearly emphasized that fish dispersal and habitat capacity in riverine ecosystems are both key drivers of fish diversity and distributions at a large spatial scale. This result has direct conservation implications. For example, neutral metacommunity models could be used to predict regional changes in biodiversity as a result of changes in river run-off associated with climate change. However, as we will discuss shortly with respect to species-discharge models (see Challenge 3), neutral models applied in this way do not estimate proximate extinction rates but instead predict extinctions after a significant time lag.

The UNTB has generated substantial controversy and, despite its numerous weaknesses, has played an important role in uniting ecology and biogeography. The key issue in the ongoing debate about neutrality is whether differences among species are important in shaping patterns of species abundance and distribution. Although this theory would seemingly be important from an applied perspective, its implications for biodiversity conservation remain unclear. *Sensu stricto*, the UNTB implies that species extinctions or invasions should not reduce biodiversity as long as dispersal among communities is maintained at appropriate levels. Clearly, more research is needed to explore the potential relevance of the UNTB to freshwater conservation biogeography.

The niche conservatism hypothesis

The degree to which plants and animals retain their ancestral ecological traits and environmental distributions ('niche conservatism') is hotly debated. The niche conservatism hypothesis is founded on the observation that many aspects of the fundamental niche (*sensu* Hutchinson, 1957) may be

conserved over long evolutionary time-scales, because the rate of adaptation to conditions outside of the niche is slower than the extinction rate (Wiens & Graham, 2005). Whether a species ecology is evolutionarily labile or conserved across space and time is a question of heightened interest in conservation biogeography, in part because of its relevance to the fate of native and non-native species facing climate change. More generally, niche conservatism has important implications in studying allopatric speciation, historical biogeography and exploring patterns and mechanisms of species richness and assemblage structure at broad spatial scales (Wiens & Graham, 2005).

Recent studies of species invasions have both supported and challenged the niche conservatism hypothesis (Wiens & Graham, 2005; Losos, 2008; Pearman *et al.*, 2008). A recent investigation into more than 11 000 vascular plants from across the Southern Hemisphere supported niche conservatism at a global scale, where only 3.6% of the evolutionary divergences associated with colonization involved a shift of biome (Crisp *et al.*, 2009). This finding suggests that many species have only a limited capacity to adapt to new environments, making them particularly susceptible to ecological change (also see Peterson *et al.*, 1999). The general assertion that niches are conserved has been countered by a number of other studies based on comparisons of microhabitat preferences, morphometric variation among individuals and environmental niche models (Wiens & Graham, 2005). More recently, research has shown that non-native species were able to establish and spread into new localities that were climatically distinct from those encountered within their native range (e.g., Broennimann *et al.*, 2007). This has led some to argue that climate niches are not static inasmuch that niche dimensions or position can shift over time and in space. At least two non-mutually exclusive mechanisms can be put forward to explain such patterns: (1) rapid evolution of species faced with novel environments, which may allow them to advance beyond the limits of their current climate distribution (i.e., a shift of both a realized and fundamental niche) and (2) ecological release from natural enemies and competitors, resulting in a higher tolerance of extreme abiotic conditions in novel habitats (i.e., a shift of a realized niche inside the boundaries of the fundamental niche) (Pearman *et al.*, 2008).

To date, it remains unclear whether the ecological niches of freshwater fishes are conserved or show rapid evolution. An initial exploration of this question was conducted by McNyset (2009) who used species distributional modelling to test for niche conservatism in six groups of North American freshwater fishes, assuming that high prediction success for sister species by reciprocal models provides evidence for niche conservatism. This study found that over moderate evolutionary time-scales, ecological niches have been conserved (with the possible exception of black basses of the Centrarchidae), thus providing a theoretical basis for a variety of analyses including the projection of species distributions in response to climate change and forecasting the spread of invasive species (discussed in greater detail in subsequent challenges).

In summary, the widespread introduction of freshwater fishes provides an opportunity to conduct natural, large-scale experiments to test the hypotheses of niche conservatism by comparing species–environment relationships between native and introduced geographic ranges. Moreover, the extensive history of fish species invasions allows for the exploration of how niche conservatism may vary temporally and geographically. Future research in this field will have important conservation implications. For instance, the balance between niche conservatism and niche shift will determine our ability to predict future locations where known high-impact invaders could successfully establish.

CHALLENGE 2: ADVANCING A TRAIT-BASED BIOGEOGRAPHY OF FRESHWATER FISHES

Biogeography has predominantly been studied from a taxonomic perspective, but over the past two decades, ecologists have increasingly found that species traits, rather than taxonomic species, may be a more powerful currency of investigation. For freshwater fishes, there is growing interest in the biogeography of functional traits – characteristics of an organism that are linked with its fitness or performance (reviewed in Winemiller, 2005). The study of trait distributions can be used to understand complex phenomena, including why organisms live where they do, how many taxa can coexist in a given place, and how they will respond to environmental change. We view the advancement of trait-based biogeography of freshwater fishes as a primary challenge and exciting opportunity for the future. We briefly illustrate two recent advances below.

Trait-based community assembly has been forwarded as a conceptual model for understanding broad-scale patterns in assemblage structure. This is supported by the basic premise that organisms with similar traits will share similar niche requirements and will therefore be ‘sorted’ into similar environments. Recent studies have provided encouraging insight into the utility of trait-based assembly theory for freshwater fishes. Irz *et al.* (2007) found evidence for environment-driven convergence in fish assemblage reproductive traits (but not trophic traits) in lakes of France and the north-eastern United States. Ibañez *et al.* (2009) showed that the proportion of invertivorous and omnivorous species decreased and increased, respectively, from upstream to downstream reaches in both temperate and tropical streams. Similarly, Olden & Kennard (2010) found that the life histories of fishes in the southern United States and eastern Australia have converged along similar gradients in hydrologic variability and productivity. From an applied perspective, these results have important implications for the development of biological indicators of river ecosystem integrity, which are often based on functional characteristics of fish assemblages (Karr & Chu, 1999). For instance, whether such indicators can be applied at intercontinental scales is an important research question, because it would inform us whether phylogenetically unrelated communities will respond similarly to future environmental

changes. Recent attention has also focused on developing and applying indices of functional diversity (i.e., functional richness, evenness and divergence) to allow for a more mechanistic approach to testing ecological theory (Villéger *et al.*, 2008). For example, Mason *et al.* (2008) included information on the trait diversity and overlap of lake fish communities in France to test whether the physiological tolerance and niche specialization hypotheses can explain species richness gradients.

Trait-based approaches have great potential to advance conservation biogeography, but only a few studies of freshwater fishes have been conducted to date. A trait-based framework provides a mechanistic basis for quantifying the link between functional trait variation and ecosystem processes that support biodiversity. Furthermore, increasing knowledge on the functional characteristics of invasive species and native species of invaded assemblages would help elucidate the roles of biotic factors in the establishment process. Given high consistency in the identification of functional traits, such as life history strategies, in freshwater fishes (e.g., Winemiller & Rose, 1992; Olden *et al.*, 2006; García-Berthou, 2007; Frimpong & Angermeier, 2009), synthetic treatments of trait–environment relationships within a biogeographic context should be on the horizon.

CHALLENGE 3: QUANTIFYING EXTINCTION RISK AND LOSS OF FISH BIODIVERSITY IN A CHANGING ENVIRONMENT

Identifying fish species at risk of extinction

One of the primary goals of conservation biology is to understand the ecological mechanisms that can render some species more vulnerable than others to population decline, range contraction and extinction (Caughley, 1994). Recent efforts have focused on endogenous (life history, dispersal and tolerance) traits that are repeatedly associated with high likelihood of extinction, with the goal of safeguarding the most vulnerable native species (O’Grady *et al.*, 2004). Previous studies have shed considerable insight into the trait correlates of extinction risk for freshwater fishes (e.g., Angermeier, 1995; Olden *et al.*, 2006, 2007, 2008a), and although the patterns are diverse, a general suite of ‘extinction-prone’ traits have emerged. Winemiller (2005) cited evidence that two life history strategies are most at risk: (1) small opportunistic species (short life span with high reproductive effort) with limited geographic ranges and (2) larger periodic species (annual spawning of large clutches and naturally episodic recruitment with large-scale spatial variation) with migratory tendencies that are impacted by reduced ecosystem connectivity from dams, levees or other hydrological alterations. In support of these predictions, Olden *et al.* (2006) found that century-long modifications to flow regimes in the Lower Colorado River Basin of the south-western United States have lead to greater distributional declines of native species characterized by the opportunistic-periodic continuum of traits. This axis defines a gradient of reproductive ‘bet-hedging’

that is considered adaptive in temporally or spatially variable environments. Large dams within the Colorado Basin have greatly reduced both spatial and temporal variation of fluvial habitats to the detriment of native fish populations.

Although the number of studies has increased in recent years, we believe that understanding of the specific mechanisms by which functional traits predispose fish species to extinction remains poor. Extinction predictions would be improved by analysing how functional traits individually and collectively predispose species to the stages of the extinction process: rarity, risk of local extirpation and vulnerability to global extinction (Olden *et al.*, 2008a). In this regard, fish life history strategies provide a useful framework, because they can be interpreted as being adaptive with respect to abiotic and biotic environmental variation in space and time (Winemiller, 2005). Exciting opportunities exist for meta-analysis of compiled functional trait databases (e.g., Frimpong & Angermeier, 2009); however, we are still challenged to develop a more predictive traits-based approach to community ecology (McGill *et al.*, 2006). Fish ecologists have been largely unsuccessful in identifying robust traits that confer differential resistance and resilience to environmental change. Ideally, such traits should be evolutionary labile and reveal low phylogenetic constraint (Poff *et al.*, 2006). Advances in these areas surely will aid development of a more mechanistic understanding of the environmental drivers of fish distribution and abundance.

Forecasting losses to freshwater fish diversity

The Theory of Island Biogeography (MacArthur & Wilson, 1967) has been widely applied to identify biodiversity hotspots, guide the delineation of terrestrial protected areas and predict the impacts of habitat loss and fragmentation on native diversity (see Whittaker & Fernández-Palacios, 2007). A central tenet of this theory is the use of the species–area relationship, which is often described as the positive relationship between species richness and island area caused by the influence of area-dependent extinction rates and habitat diversity. River basins and lakes are considered biogeographic islands, where habitat ‘size’ can be defined by river discharge or lake volume (Xenopoulos *et al.*, 2005; McGarvey & Ward, 2008).

The species–area relationship has been used to predict species extinctions at large spatial scales (Rosenzweig, 1999). For river basins, fish species losses can be extrapolated by, in effect, sliding down the curve describing an empirically derived species–discharge relationship (SDR) in accordance with assumptions about future decreases in annual discharge. This approach has been applied at basin and sub-basin scales in Australia (Poff *et al.*, 2001) and the United States (Xenopoulos & Lodge, 2006). It has also been applied at the global scale by Xenopoulos *et al.* (2005), who developed a SDR for 295 river basins to predict fish species extinctions that would result from flow reductions that may result from continued climate change and increased water withdrawals for human use. According to this study, projected reductions in discharge may eliminate up to 75% of the fish species in a given river basin. Predictions

obtained from SDRs, however, must be interpreted with caution for at least five reasons.

First, SDRs assume that species richness is in equilibrium with discharge; a supposition that is likely to be violated in many regions where fish species extinctions related to past historical events (e.g., glaciations) are not fully balanced by colonization from neighbouring river basins (Hugueny *et al.*, 2010). Even when this assumption is plausibly met, such as for tributaries that drain into larger rivers, it is difficult to assess how long it will take to reach a new equilibrium after some change in discharge. In other words, this approach does not provide true extinction rates but instead a percentage of species ‘committed to extinction’ (see next challenge) with an unspecified time-lag. Second, using SDR models to predict extinction events requires one to extrapolate beyond the range of their empirical data (Botkin *et al.*, 2007) and to assume that fishes will not rapidly adapt to new hydrologic conditions. Projected changes in stream flow associated with climate change and human water needs are highly uncertain (Palmer *et al.*, 2008), and the influence of habitat connectivity on dendritic stream networks adds an additional layer of complexity to such extrapolations (Fagan *et al.*, 2002). Third, mean annual discharge is a simplified estimate of the total habitat available to fish species. For example, intermittent (arid and semi-arid) streams have much lower fish richness than perennial streams of similar catchment size, probably attributed to high variation in run-off and occasional extinctions because of stream desiccation and flash floods (Poff *et al.*, 2001). Fourth, the SDR is sensitive to the spatial scale of sampling, which renders applications across multiple scales difficult. Scale dependence has direct conservation implications as noted by McGarvey & Ward (2008), whereby shallow SDR slopes, derived without accounting for scale, underestimate future extinctions. A fifth limitation with these models is that total species richness in many rivers has greatly increased because of the establishment of non-native species, typically without concurrent extinction of native species (Leprieur *et al.*, 2008). This finding, along with the fact that the proportion of total fauna composed of non-native species varies greatly from basin to basin, undermines the key equilibrium assumption of species saturation needed to support the validity of SDRs predictions. In summary, we believe that SDRs have the potential to generate quantitative estimates of species losses because of future environmental change. But we caution that the critical assumptions discussed above have yet to be fully explored. Research in this area should be a priority.

CHALLENGE 4: EVALUATING THE MAGNITUDE AND GEOGRAPHY OF EXTINCTION DEBT FOR FRESHWATER FISHES

Although the effects of habitat degradation, climate change or invasive species can lead to immediate extinction, there is often a considerable lag between the environmental change and when extinctions occur. These delayed extinctions have been called ‘extinction debts’, referring to the number or proportion

of species (or populations) expected to go extinct as the assemblage reaches a new equilibrium following an environmental disturbance (Kuussaari *et al.*, 2009). This term was popularized by Tilman *et al.* (1994) in the context of metapopulation models, but its origins trace back to the Theory of Island Biogeography (MacArthur & Wilson, 1967) and the concept of relaxation time to describe temporal changes in a system from one equilibrium condition to another (Diamond, 1972).

Extinction debt has recently emerged as a major conservation concern (Kuussaari *et al.*, 2009; Jackson & Sax, 2010). Extinction debt communicates the concept that species may initially survive environmental change but many remnant populations may be committed to eventual extinction through a combination of deterministic and stochastic processes. In the simplest case, a population in which mortality slightly exceeds natality will ultimately go extinct, but it may take a considerable amount of time for this to happen, especially for long-lived species. We discuss one possible example below.

The Colorado River Basin supports one of the most distinctive fish communities in North America, including the federally endangered humpback chub *Gila cypha*. Following completion of Glen Canyon Dam in 1963, this long-lived fish (maximum longevity = 40 years) was extirpated throughout much of its native range in the Lower Colorado River (Coggins *et al.*, 2006). Despite diminished reproductive success and juvenile survival caused by multidecadal alterations to flow (daily fluctuations caused by hydroelectric operations), temperature (cold hypolimnetic releases from Lake Powell), sediment regimes and biological interactions involving a plethora of invasive fish species, the humpback chub continues to persist in the Colorado River (Coggins & Walters, 2009). One possible explanation is that chub populations retreat to suitable remnant habitats within the Grand Canyon and near the confluence of Little Colorado River, thus slowing a process of population decline and competitive displacement that might ultimately lead to extinction. Although persistent threats induce significant impacts on these remnant populations, transient natural or human-created flow events that create low velocity, warm-water conditions along structurally complex shorelines may lead to recruitment pulses which facilitate persistence. This explanation is supported by a recruitment surge of humpback chub in the late 1990s or early 2000s that may have resulted from greater habitat availability for juvenile rearing in the Grand Canyon (although non-native fish control has also been a management practice). Recent evidence suggests that the number of adult humpback chub in Grand Canyon stabilized during years 2001–05, following more than a decade of decline (Coggins & Walters, 2009). Perhaps the extinction debt has been paid, or perhaps this apparent population gain is merely a short-term response to a transient event. What is certain is that our ability to answer this question is critical for assessing how much time is left to implement conservation measures such as habitat improvement, non-native fish removal and environmental flow releases.

Has the ecological degradation of the world's rivers created an extinction debt? If so, when and where will this debt be paid? To date, empirical investigations into extinction debt for freshwater fishes are scarce (but see Harding *et al.*, 1998). Future research is needed to evaluate how the probability and magnitude of extinction debt varies as a function of fish life history traits, spatial and temporal habitat patterns and the timing of past environmental changes. This would significantly contribute to a generalized understanding of biodiversity loss. Some argue that to identify extinction debts may require more time than we have remaining for taking measures to prevent them (Malanson, 2008). It might be possible to quantify extinction debt based on long-term data on species occurrence or to estimate debt by comparing past versus present habitat characteristics, present-day stable versus unstable landscapes or using modelling approaches such as population viability analysis (Brook *et al.*, 2000; Kuussaari *et al.*, 2009). Moreover, research could focus on quantifying differences between the realized and fundamental niches of endangered species to estimate extinction debt (i.e., larger differences predict greater debts). Trait-based approaches (Challenge #2) and species distribution modelling (Challenge #6) are two potential avenues for estimating and comparing the dimensions of the realized and fundamental niche.

The concept of extinction debt is consistent with the precautionary principle of risk management, but it remains to be seen if it is just a theoretical construct or a robust paradigm to guide conservation. The answer is critical, because many fish species may already be doomed to become locally, regionally or globally extinct (Olden *et al.*, 2007). In the worst case, if environmental conditions change so that species cannot reproduce locally, the debt may be too large, and the timeline to extinction will be determined by the longevity of the remaining individuals. By understanding the extinction debt, efforts could be concentrated on improving conditions in those areas where chances for long-term population persistence are greatest. A repercussion of not properly accounting for extinction debt is that we may not be able to differentiate impacts of multiple stressors, each with its own time course, on native species. Complicating matters further is the need to assess both sides of the biodiversity ledger: extinction debt and the invasion process (Jackson & Sax, 2010) (also see Challenge #5).

CHALLENGE 5: ELUCIDATING THE PATTERNS AND DRIVERS OF FRESHWATER FISH INVASIONS

Changing source regions, vectors and geographic routes of fish introductions

In recent decades, human activities have greatly increased the frequency and spatial extent of fish species introductions worldwide. Species have been intentionally introduced for a variety of reasons, such as recreational fishing and biological control, and unintentionally through ballast-water discharge from international shipping, bait-bucket releases by

recreational anglers, ornamental fish trade and escapes from fish farms (Rahel, 2007). It is also increasingly apparent that the number and routes of dispersal pathways are highly dynamic in both time and space (Moyle & Marchetti, 2006). In the Laurentian Great Lakes, invasions caused by deliberate releases (e.g., fish stocking) have declined over the past 100 years, whereas invasions related to shipping, pet trade and other unintended release have increased (Ricciardi, 2006). Although this general trend from intentional to unintentional introductions is true of many developed countries, most developing countries are still in an active phase of intentional stocking and are highly vulnerable to the unplanned invasions that often accompany economic growth.

With economic globalization, trade connections are increasing between regions, and these connections result in more introductions of non-native species (Perrings *et al.*, 2005). Developing countries are now facing significantly greater risks of biological invasions. For instance, introduction rates have greatly increased in Brazil as a result of reservoir stocking programmes, aquaculture, sport fishing, control of disease vectors and the pet trade (Vitule *et al.*, 2009). The hundreds of new and planned hydropower dams in large rivers of many developing countries will likely be accompanied by increasing rates of non-native fish introductions via stocking programmes and promoting secondary spread from other infested waters (Johnson *et al.*, 2008). Similarly, channel construction creating new connections between neighbouring river basins (e.g., for water transfer and navigation purposes) are also likely to enhance human-mediated dispersal of species (Galil *et al.*, 2007).

Changing pathways of fish introductions represents an equally important challenge. In recent decades, the ornamental pet trade has emerged as a major pathway for freshwater fish introductions (Padilla & Williams, 2004). In contrast to aquaculture and sport-fish introductions that normally involve only the most 'popular' species (e.g., tilapia, trout), the ornamental fish trade involves thousands of species. For instance, the United States imported over 1 billion living fishes for commercial purposes (e.g., ornamental fishes) between 2000 and 2005, with half of these being freshwater species from tropical regions (Smith *et al.*, 2008). Ornamental fishes have received minimal attention from regulatory agencies, with poor record keeping of the type and number of organisms imported (Smith *et al.*, 2008). Given uncertainty in the taxonomy of many ornamental fishes, risk analysis to prevent intercontinental introductions of non-native species consequently is limited. Identifying source regions and pathways of fish trade would help guide conservation strategies aimed at preventing introductions of non-native fishes across large geographic distances.

Revealing the drivers of non-native fish richness at continental and global scales

Identifying the dominant drivers of non-native species richness is a key challenge in conservation biogeography (Whittaker *et al.*, 2005). Three non-mutually exclusive hypotheses have

been proposed to explain broad-scale patterns in non-native species richness. First, the 'human activity' hypothesis predicts that, by disturbing natural landscapes and increasing the importation and dispersal of non-native species, human activities facilitate greater levels of establishment. Second, the 'biotic acceptance' hypothesis predicts that the same factors that support greater native richness in a region (e.g., abundant resources and habitat heterogeneity) also promote the establishment of non-native species. Third, the 'biotic resistance' hypothesis predicts that communities with many native species will be more resistant to non-native species because of competitive exclusion and an increased likelihood of encountering native predators. Reconciling the relative role of these hypotheses using observational, experimental and theoretical studies has been a focus of continued research activity (Fridley *et al.*, 2007).

In a global analysis, Leprieur *et al.* (2008) showed that patterns of non-native fish richness for 1055 major river basins was best explained by the 'human activity' hypothesis. Specifically, non-native fish richness is positively correlated with gross domestic product (GDP), which in turn reflects levels of human economic activity and infrastructure, including roads, canals, railways and dams. However, the exact mechanism underlying the relationship between non-native fish diversity and economic activity remains unclear. For instance, the high number of non-native fishes found in regions with high GDP may be attributed to greater propagule pressure (i.e., more potential invaders are deliberately or accidentally transported to the area) or to environmental degradation. Studies conducted at the smaller, reach scale support the greater importance of biotic resistance (Mitchell & Knouft, 2009), reinforcing the scale dependence of this phenomenon. Consequently, additional research is needed to disentangle the relative importance of different environmental drivers in shaping patterns of non-native fish species richness, including the influence of spatial scale (Blanchet *et al.*, 2009).

CHALLENGE 6: FORECASTING THE FUTURE GEOGRAPHY OF FRESHWATER FISHES

Niche concepts and theory, in the form of species distribution models (SDMs) or ecological niche models, have become central in efforts to understand how future environmental change may impact species and their habitats (Elith & Leathwick, 2009). Broadly, these models derive relationships between species presence-absence data and suites of environmental variables to forecast species distributions in space (e.g., in an alternate region) or time (e.g., under a climate change scenario). This is typically accomplished using a Geographic Information System to project the species' distribution based on its predicted response to a map of environmental factors (i.e. the 'Grinnellian niche').

SDMs seem to perform well in characterizing natural species distributions, particularly when data from well-designed surveys and relevant environmental predictors are analysed

with an appropriately specified model (Elith & Leathwick, 2009). Although a number of studies have applied SDMs to predict potential geographic ranges of invasive freshwater fishes, only recently have these models been used to predict future distributions as a consequence of climate change (e.g., Chu *et al.*, 2005; Buisson *et al.*, 2008). Buisson *et al.* (2008) used presence-absence records in French river systems to predict the future distributions of 30 fish species under several climate change scenarios. Their results suggest that cold-water species would experience the greatest climate-induced reductions, whereas climate change would create new opportunities for some cool-water and warm-water fish species. Additional studies include Herborg *et al.* (2007) who identified high-risk areas for the establishment of 14 invasive species of snakehead (Channidae) in North America, and Sharma *et al.* (2007) who predicted a northward expansion of lakes in Canada that will be suitable for smallmouth bass, *Micropterus dolomieu*, under a future climate change scenario.

Despite the fact that SDMs have become popular in recent years, they remain subject to criticism, because they implicitly assume that species are in equilibrium with their environment, and they often fail to incorporate dispersal, demographic processes and biotic interactions (e.g., Dormann, 2007; Jeschke & Strayer, 2008). These assumptions are likely to be unrealistic for fishes in freshwater ecosystems for a variety of reasons, including priority effects and other historical contingencies, dispersal limitation, disturbance regimes yielding non-equilibrium population dynamics, nonlinear species interactions and time-lags in population responses. For instance, assuming that all the 30 studied fish species have the same dispersal ability, Buisson *et al.* (2008) acknowledged that their models present limitations, as some species will not be able to disperse at a sufficient rate to track future climate conditions. We therefore strongly encourage future studies to incorporate dynamic processes, such as dispersal, in SDMs (e.g., Engler *et al.*, 2009).

Another critical issue is the role of functional traits in determining species responses to environmental change (Kearney & Porter, 2009). Functional traits of freshwater fishes reveal consistent patterns, independent of taxonomy, in relation to environmental factors from local to regional scales (Winemiller, 2005). This observation suggests that advances in the development of SDMs for freshwater fishes will likely involve the coupling of physiological constraints and environmental data to provide a mechanistic view of species functional niches (see Challenge 2). Extending this by taking advantage of theoretical developments in macroecology, life history theory, bioenergetics and food-web ecology offers exciting potential to predict assemblage- and community-level responses to environmental change over regional and global scales. For example, Jennings *et al.* (2008) outlined an approach to forecasting the collective properties of marine fish communities (i.e., biomass, production, size and trophic structure), which should be transferable to the freshwater realm. In common with recent syntheses on this topic, we believe that a more wide-ranging approach to linking theory, data and models would bring substantial benefits.

CHALLENGE 7: UNDERSTANDING THE INTERACTIVE EFFECTS OF MULTIPLE STRESSORS IN FRESHWATER ECOSYSTEMS

In a synopsis of the sources of human-caused extinction, Soulé (1991) described a 'sinister sextet' of major sources of global species loss, which in freshwater ecosystems includes habitat loss, species invasions, overharvesting and climate change (Allan & Flecker, 1995). Mitigation of these direct threats continues to be a clear focus for conservation biology, but with an increasing recognition that synergistic effects among stressors may hasten the extinction process (Didham *et al.*, 2007; Brook, 2008). Abundant evidence suggests that each of the aforementioned impacts can independently increase the risk of extinction faced by freshwater fishes (Dudgeon *et al.*, 2006), yet our understanding of their interactive effects (i.e., are they additive or multiplicative?) is just now emerging (e.g., Ormerod *et al.*, 2010 and references therein). The interaction between species invasions and climate change is a chief example, whereby altered thermal and flow regimes, reduced ice cover in lakes and increased canal and reservoir construction (among other factors) associated with projected climate change may alter the pool of potential colonists, influence the probability of establishment and impact of non-native species and require the initiation or expansion of prevention and control efforts (Rahel & Olden, 2008). For instance, Johnson *et al.* (2008) showed that non-native species were 2–300 times more likely to occur in impoundments than in natural lakes and impoundments enhance the invasion risk posed to natural lakes by increasing their proximity to invaded water bodies. Furthermore, climate-induced changes to water availability and increasing human demand for water are likely to prompt the construction of new reservoirs to increase water supplies in many regions (Palmer *et al.*, 2008), thus enhancing future opportunities for species invasions. Overall, empirical evidence supporting many of the hypothesized linkages between climate change, habitat loss and invasive species remains scant. Process-based models offer one approach to predicting ecological responses to multiple interacting stressors. For instance, Nelson *et al.* (2009) combined several mechanistic models to predict the interactive effects of future climate change and urbanization on freshwater fish assemblages. However, the ability to account for feedbacks, non-linear behaviour and uncertainty in such models remains extremely challenging. We encourage greater research effort aimed at improving our understanding of these interactions for freshwater fish biogeography.

CHALLENGE 8: QUANTIFYING NEW FEATURES OF THE BIODIVERSITY CRISIS: FISH FAUNAL HOMOGENIZATION AND THE EMERGENCE OF NOVEL ASSEMBLAGES

For many years, the biodiversity crisis has been synonymous with the loss of species through global extinction. At subglobal scales, however, localized extirpations and non-native

invasions are equally important, pressing problems (Sax & Gaines, 2003). In the wake of continued human-driven species invasions and extinctions, the process of biotic homogenization has rapidly emerged as a topic of interest in conservation biogeography (Olden, 2006). Biotic homogenization refers to a regional decrease in beta-diversity over time, resulting from the spread of cosmopolitan species and/or loss of native endemics. This is a unique research challenge, because it is a multifaceted process that subsumes many aspects of the modern biodiversity crisis, including species invasions, extirpations and environmental alteration (McKinney & Lockwood, 1999).

Recent years have witnessed increased efforts to quantify biotic homogenization across taxonomic groups – a trend that started with freshwater fishes. In a landmark study, Rahel (2000) compared the similarity of regional (state) fish faunas in the United States between present-day and pre-European settlement periods and found that individual pairs of regions averaged 15 more species in common now than they did in the past (on average, fish faunas became more similar by 7.2%). Most striking was that 89 pairs of regions with zero historical similarity (no species in common) now share, on average, over 25 species. In the past decade, broad-scale patterns of homogenization have been evaluated for other regions, including Canada (Taylor, 2004), Australia (Olden *et al.*, 2008b) and Europe (Clavero & García-Berthou, 2006) in addition to a number of regional-scale studies (see review by Olden, 2006). In contrast to taxonomic homogenization, the study of functional homogenization (i.e., replacing native species that fill ‘specialist’ roles with non-native ‘generalist’ species) has received relatively little attention. Functional homogenization is expected to have important implications for community and ecosystem properties, thus it deserves greater attention from ecologists.

Biotic homogenization is an important dimension of the modern biodiversity crisis having significant ecological, evolutionary and social implications (Olden *et al.*, 2004). To date, we have begun to better understand patterns of biotic homogenization for freshwater fish; however, we still know very little about the mechanisms and consequences of this phenomenon. For example, environmental change ultimately promotes the geographic expansion of some species and the reduction in others, leading to biotic homogenization (McKinney & Lockwood, 1999), yet formal investigations into these relationships are rare (but see Olden *et al.*, 2008b). Future studies should examine the homogenization process for different community properties (species occurrence, abundance and traits) at multiple spatial and temporal scales, with careful attention paid to the various biological mechanisms (invasions versus extinctions) and environmental drivers (environmental alteration versus biotic interactions) involved.

Increased homogenization of biotas associated with the massive and accelerating movement of species within regions is also likely to contribute to the creation of novel assemblages. Novel assemblages, sometimes referred to as ‘no-analogue’ or ‘emerging ecosystems’, are communities that consist of species that did not previously co-occur (Hobbs *et al.*, 2006).

Technically, any assemblage that has lost native species or gained non-native species is ‘novel’, but some assemblages have been transformed to such an extent that they are on the verge of becoming entirely new assemblages (Williams & Jackson, 2007). One of the biggest issues raised by changing climates is whether species whose preferred climates disappear locally can migrate to other areas where suitable climates still persist. Future predictions of the composition and geography of novel assemblages will therefore need to account for both native and non-native species’ responses to environmental change. The combination of novel fish assemblages and altered biophysical conditions will result in new systems with their own structural and functional characteristics.

CHALLENGE 9: PROMOTING SCIENTIFIC RIGOUR IN EMERGING FRESHWATER FISH CONSERVATION STRATEGIES

If climate change proceeds over the next century as current models predict, then many species will be forced to rapidly adapt to their new environments, to migrate to more suitable habitats, or face extinction (Parmesan, 2006). Freshwater fishes will, however, face a particularly large number and variety of both natural and artificial obstacles to movement when attempting to migrate latitudinally or along elevational gradients to remain within thermally suitable habitats. Hundreds of thousands of dams, diversions and impassable road culverts exist globally, and fishes have limited abilities to pass these barriers. Increasingly, small diversions and culverts under roadways are being modified to allow for movement of fishes in response to environmental change; however, this simultaneously increases the risk of invasion by non-native species and associated diseases, which are major threats to native species persistence (Fausch *et al.*, 2009).

In contrast to traditional management approaches that aim to increase landscape connectivity, a recently suggested conservation strategy involves managed relocation – also referred to as assisted migration or translocation (Hoegh-Guldberg *et al.*, 2008). This strategy involves moving individuals from areas of current occupancy that are at imminent risk to climate change to new locations, outside of their native range, where the probability of long-term survival is thought to be higher (Richardson *et al.*, 2009). While many hail managed relocation as pragmatic and forward-thinking, the proposition of intentionally moving species to address climate change has understandably raised concerns and sparked debate (Ricciardi & Simberloff, 2009). Despite the flurry of recent interest, however, the discussion of managed relocation has, to date, focused almost entirely on terrestrial organisms, with little consideration given to freshwater biota (but see Olden *et al.*, in press). In contrast to many terrestrial species, freshwater fishes are uniquely constrained in terms of responding to climate change by being limited to dispersal along fluvial corridors consisting of rivers, ponds and lakes with varying degrees of connectivity. These distinctive properties of freshwater ecosystems may therefore make managed relocation an indispensable

conservation strategy for reducing the threat of climate-driven extinctions. However, these are the same properties that make the approach particularly risky in terms of unintended ecological consequences (e.g., the insular nature of freshwater systems makes them highly sensitive to the detrimental effects of introduced species; Dudgeon *et al.*, 2006; Rahel, 2007; see Challenge 5). Guidelines for fish reintroductions are emerging (George *et al.*, 2009), but much more research is needed to determine specific cases in which this conservation strategy would be justified.

CHALLENGE 10: IMPROVING CONSERVATION PLANNING STRATEGIES FOR FRESHWATER FISH SPECIES

As human activities continue to alter freshwater ecosystems globally, a critical conservation goal is to develop dynamic biodiversity conservation management strategies that can adapt to changing environmental conditions while maintaining natural biogeographic patterns in biota (McClanahan *et al.*, 2008). Until recently, comparatively little effort has been devoted to the design and implementation of freshwater conservation management frameworks (Abell *et al.*, 2007). Instead, uninformed opportunism (*sensu* Pressey & Bottrill, 2008) has reigned, whereby conservation of freshwater ecosystems is tangential to conservation goals developed for terrestrial ecosystems. Spatial patterns of species richness and endemism have often been used to guide the conservation of freshwater fish biodiversity (e.g. Chu *et al.*, 2003); however, such approaches do not provide the flexibility needed for an adaptive and complex conservation planning process. Conservation planning that incorporates complementarity (a gain in biodiversity when a site is added to an existing set of protected areas) yields more efficient and cost-effective conservation than ad-hoc scoring or ranking strategies (Margules *et al.*, 2002).

Systematic conservation planning aims to efficiently select a comprehensive and representative set of areas for conservation management to ensure the long-term persistence of biodiversity (Margules & Pressey, 2000). Criteria such as size, shape, alignment, replication, connectivity and dispersion are seen as critical to the persistence of biodiversity and should guide the spatial configuration of conservation area networks (Margules & Pressey, 2000; Sarkar *et al.*, 2006). Despite the prominence of protected areas as conservation interventions for terrestrial and more recently marine features, systematic approaches have only recently been applied to freshwater ecosystems (e.g., Linke *et al.*, 2008; Moilanen *et al.*, 2008; Nel *et al.*, 2009a; Hermoso *et al.*, 2010). These studies have highlighted a number of significant challenges (reviewed in Nel *et al.*, 2009b) for effective conservation planning because of the distinctive properties of freshwater systems and their influence on spatial and temporal patterns of biodiversity. Successfully conserving freshwater fish biogeographical patterns is also contingent on addressing many of the challenges listed elsewhere in this paper. Here, we highlight several research areas needed to support systematic conservation planning for freshwater fishes.

Fish have commonly been used as surrogates for biodiversity in freshwater conservation planning, possibly because the distribution and ecological requirements of fish are comparatively well understood relative to most other freshwater-dependent biota. Yet, the extent to which fish are effective surrogates for other aquatic biota, and hence appropriate targets for conservation planning have not been comprehensively evaluated (Rodrigues & Brooks, 2007). Other biodiversity measures based on fish functional traits (functional diversity) and phylogenetic relationships (phylogenetic diversity) should provide useful insights. Alternative extinction scenarios can be expressed as potential losses in 'feature diversity' in regard to the evolutionary history of the studied region and may hence guide conservation priorities (Faith & Baker, 2006). The major challenge here is to assess the level of spatial congruence between biodiversity measures and subsequent implications for prioritizing a network of freshwater areas for conservation management.

The consideration of connectivity and its importance in maintaining natural ecological processes and biodiversity in freshwaters is also key to effective conservation planning for these systems (Hermoso *et al.*, 2010). Designing efficient conservation area networks in freshwaters is challenging because of the spatial hierarchies of fluvial ecosystems and networks and the necessity to consider longitudinal, lateral and surface/groundwater connections (Fausch *et al.*, 2002). Evaluation of directional connectivity requirements based on knowledge of species life history traits, including migration patterns, offers one promising approach (Moilanen *et al.*, 2008).

Finally, setting scientifically defensible conservation targets (e.g., the number of populations or areas required to maintain species) is challenging, because minimum population sizes or minimum habitat requirements for most freshwater species are not known (Nel *et al.*, 2009a). Multiple occurrences in different catchments allow for different genetic lineages to be conserved (Nel *et al.*, 2009a); however, conservation plans must go beyond mere spatial configurations to address human-induced stressors (Araújo, 2009). Better integration of ecological principles (e.g., biogeographical theory, successional pathways and source-sink population structures; Margules & Pressey, 2000; Sarkar *et al.*, 2006) is needed for conservation of freshwater fishes in an ever-changing world.

CONCLUSION

Reflecting upon fish conservation biogeography, we believe that our ability to meet future challenges will benefit from what we call the Janus-approach. In Roman mythology, Janus was the god of gates, doors, doorways, beginnings and endings and is most often depicted as having two faces or heads, facing in opposite directions; one viewing what is behind and the other looking towards what lies ahead. In modern culture, his most prominent namesakes are the month of January, which begins the New Year, and the janitor who is a caretaker of doors and halls. To us, Janus reminds us that we must always be aware of where we have been by using knowledge from historical biogeography, while at the

same time being conscious of the future in which humans continue to shape ecological patterns and processes. Achieving a delicate balance between the practice of backward reflection and forward-looking is critical for ecologists to advance the conservation biogeography of freshwater fishes.

In his role as the guardian of entrances and exits, Janus was also believed to represent new beginnings. By reflecting on recent scientific progress in fish conservation biogeography, we have identified a set of core challenges for research investment. However, this is only the start; the next step is implementation. In our view, several critical implementation issues cut across all of these challenges. These issues include deficient taxonomic (the Linnean shortfall) and geographic data (the Wallacean shortfall) required to support applied research (Bini *et al.*, 2006), the need to establish a global information system to support data integration and sharing among researchers and conservation practitioners and the requirement to make scientific research useful to decision-makers responsible for conservation policies and management. We agree with Salafsky *et al.*'s (2002) assertion that to narrow the gap between the information needed for conservation and the state of our ecological knowledge, new research projects should be attentive of the needs of end-users. With this in mind, we hope that the challenges discussed in our study offer a useful roadmap for identifying new paths of investigation into the field of freshwater fish biogeography.

ACKNOWLEDGEMENTS

The final manuscript benefited greatly from comments by D. McGarvey, T. Erös and an anonymous referee. The authors thank Dave Richardson for the invitation to participate in this special issue. Funding was gratefully provided by the USGS Lower Colorado River Aquatic GAP Program (J.D.O.), the U.S. Environmental Protection Agency Science To Achieve Results (STAR) Program (Grant No. 833834010) (J.D.O.), the Tropical Rivers and Coastal Knowledge Research Hub and the Australian Rivers Institute, Griffith University (M.J.K. and J.D.O.), the ANR 'Freshwater fish diversity' (ANR-06-BDIV-010, French Ministry of Research) (F.L. and P.A.T.), the estate of Carolyn Wierichs Kelso (K.O.W.), and the Spanish Ministry of Science (CGL 2006-11652-C02) (E.G.B.).

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BIOSKETCH

The genesis of this manuscript emerged from a symposium entitled *Species invasions, environmental change and the future biogeography of freshwater fishes* at the 10th International Congress of Ecology (Brisbane, Australia), which provided the exciting opportunity for all the co-authors to share their views on fish biogeography (and a number of other topics). See <http://www.fish.washington.edu/research/oldenlab/INTECOL2009.html>.

Author contributions: All authors contributed ideas that led to the concept for the paper; Julian Olden led the writing with significant input from all co-authors.

Editor: David Richardson