Species invasions and the changing biogeography of Australian freshwater fishes

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ABSTRACT

Aim By dissolving natural physical barriers to movement, human-mediated species introductions have dramatically reshuffled the present-day biogeography of freshwater fishes. The present study investigates whether the antiquity of Australia's freshwater ichthyofauna has been altered by the widespread invasion of non-indigenous fish species.

Location Australia.

Methods Using fish presence–absence data for historical and present-day species pools, we quantified changes in faunal similarity among major Australian drainage divisions and among river basins of north-eastern Australia according to the Sørensen index, and related these changes to major factors of catchment disturbance that significantly alter river processes.

Results Human-mediated fish introductions have increased faunal similarity among primary drainages by an average of 3.0% (from 17.1% to 20.1% similarity). Over three-quarters of the pairwise changes in drainage similarity were positive, indicating a strong tendency for taxonomic homogenization caused primarily by the widespread introduction of *Carassius auratus*, *Gambusia holbrooki*, *Oncorhynchus mykiss* and *Poecilia reticulata*. Faunal homogenization was highest in drainages subjected to the greatest degree of disturbance associated with human settlement, infrastructure and change in land use. Scenarios of future species invasions and extinctions indicate the continued homogenization of Australian drainages. In contrast, highly idiosyncratic introductions of species in river basins of north-eastern Australia have decreased fish faunal similarity by an average of 1.4%.

Main conclusions We found that invasive species have significantly changed the present-day biogeography of fish by homogenizing Australian drainages and differentiating north-eastern river basins. Decreased faunal similarity at smaller spatial scales is a result of high historical similarity in this region and reflects the dynamic nature of the homogenization process whereby sporadic introductions of new species initially decrease faunal similarity across basins. Our study points to the importance of understanding the role of invasive species in defining patterns of present-day biogeography and preserving the antiquity of Australia's freshwater biodiversity.

Keywords
Biogeography, biotic homogenization, biotic differentiation, beta-diversity, community similarity, freshwater fishes, species invasions.

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INTRODUCTION

Humans have a noteworthy ability for introducing species to areas beyond their native range, giving the potential for these non-indigenous species to become biological invaders. The continuing globalization of economies and trade has greatly facilitated this process, and non-indigenous species are spreading at unprecedented rates, crossing oceans and colonizing formerly

remote regions of the world (Perrings *et al.*, 2005). While only a fraction of non-indigenous species become invasive (Jeschke & Strayer, 2006), those that do represent a leading threat to national economies and human health, and cause tremendous ecological damage ranging from the extinction of native species to alteration of ecosystem processes (Vitousek *et al.*, 1996; Mack *et al.*, 2000; Pimentel *et al.*, 2000; Simberloff, 2001).

There is a long history of introduction of non-indigenous fishes in freshwater ecosystems, the rate of which has accelerated greatly over time as methods of transportation have improved and trade barriers have relaxed (Copp *et al.*, 2005). The motives for, and the mechanisms by which, non-indigenous species have been introduced across the globe have been many and varied. Historical motivation dates back to the Roman Empire and the extensive fish culturing of the common carp, *Cyprinus carpio*. Today, international fish introductions number in the thousands, occurring via a multitude of intentional (e.g. stocking sport fishes, aquarium and bait release) and inadvertent (e.g. aquaculture escape, ballast water transport) vectors, and whose establishment is promoted by human activities. Fish invasions are so widespread that they are now considered a significant component of global environmental change, and are recognized as a leading threat to native biodiversity (Dudgeon *et al.*, 2006).

Ecologists are now challenged to reconcile the historical biogeography of long-evolved native species with the emerging and rapidly expanding patterns of recently arrived non-indigenous species. In contrast to vagile terrestrial species, freshwater fishes are uniquely constrained because their ability to respond to environmental change is limited to movement defined by the connectivity of water. Consequently, large-scale natural range expansions of species are typically the result of rare opportunities associated with drainage rearrangement, temporary hydrological connectivity between drainages by freshwater plumes into oceans, and remote possibilities for random dispersal by 'rains' and accidental movement by terrestrial organisms (Banarescu, 1990). In recent times, however, humans have dramatically enhanced the ability of fish species to overcome these natural biogeographical barriers to movement either through intentional transport or other colonization routes created by anthropogenic activities (Rahel, 2007).

By dissolving physical barriers to movement and connecting formerly isolated regions of the world, human-mediated species introductions have dramatically reshuffled the present-day biogeography of freshwater fishes. The nature of this biological reorganization is deceptively complex because it involves the simultaneous processes of species invasions and extinctions operating in response to natural and human-induced environmental change (Olden, 2006). For example, a number of studies spanning multiple taxonomic groups have shown that the number of non-indigenous species typically surpasses the number of species extinctions in any given area, leading to elevated species richness (Sax & Gaines, 2003). Elements of this invasion–extinction equation, however, are highly non-random with respect to taxonomy and the geography and history of environmental change. In freshwater ecosystems, for example, numerous fish species of carp, trout, tilapia and sunfish have

been introduced globally (Ruesink, 2005), while highly endemic species are either threatened by or have already been driven to extinction (Harrison & Stiassny, 1999). On balance, the range expansion of ubiquitous non-indigenous species and the loss of endemic forms tend to be homogenizing faunal and floral species pools by decreasing beta-diversity (McKinney & Lockwood, 1999; Olden, 2006). Compositional changes in biological similarity with time, either increasing (homogenization) or decreasing (differentiation), have significant ecological and evolutionary consequences (Olden *et al.*, 2004) and can influence regional conservation planning (Rooney *et al.*, 2007). Recent large-scale evidence suggests that fish invasions have altered patterns of beta-diversity (Rahel, 2000; Marchetti *et al.*, 2001; Taylor, 2004), although the magnitude and direction of change varies geographically (Olden, 2006) and is dependent on the spatial and temporal scale of investigation (Olden & Poff, 2004; Cassey *et al.*, 2006; Clavero & García-Berthou, 2006). However, with the exception of North America (Rahel, 2000; Taylor, 2004), continental-scale investigations of biotic homogenization are lacking, and the environmental drivers of this process remain elusive.

The present study investigates whether the antiquity of Australia's freshwater ichthyofauna has been threatened by the widespread invasion of non-indigenous fish species over the late 19th and 20th centuries. Although relatively depauperate by world standards, with a little over 200 species, the Australian freshwater ichthyofauna has long been recognized as distinct from that of the rest of the world (Allen *et al.*, 2003). Many of the Australian freshwater fishes, although presumably well adapted to the harsh environment and pronounced seasonal fluctuations experienced in many parts of Australia, show little evidence of specialization, and lack the diversity of life-histories and characteristics of many other continents. Consequently, Australia's freshwater ecosystems are thought to be particularly vulnerable to the establishment and impact of non-indigenous fishes (Arthington, 1991). In fact, approximately one-fifth of Australian fishes are considered to be under serious conservation threat, and negative interactions with non-indigenous species are considered a significant risk to over three-quarters of these species (Australian Society for Fish Biology, 2004). Here, we address four questions concerned with fish species invasions and present-day changes in Australian biogeography. First, has the establishment of non-indigenous fish species, from both overseas introductions and native translocations, caused Australia's fish faunas to become homogenized or differentiated in space? Second, do observed patterns in faunal compositional similarity vary across different spatial scales ranging from major drainage divisions at the continental scale to coastal river basins in north-eastern Australia? Third, how are future species invasions and extirpation of threatened native species likely to shape future patterns of fish faunal biogeography? Fourth, are patterns of faunal change related to spatial variation in anthropogenic disturbance? Answers to these questions are essential for developing conservation and management policies that ensure the preservation of native fish biogeography in the light of past and future species invasions.
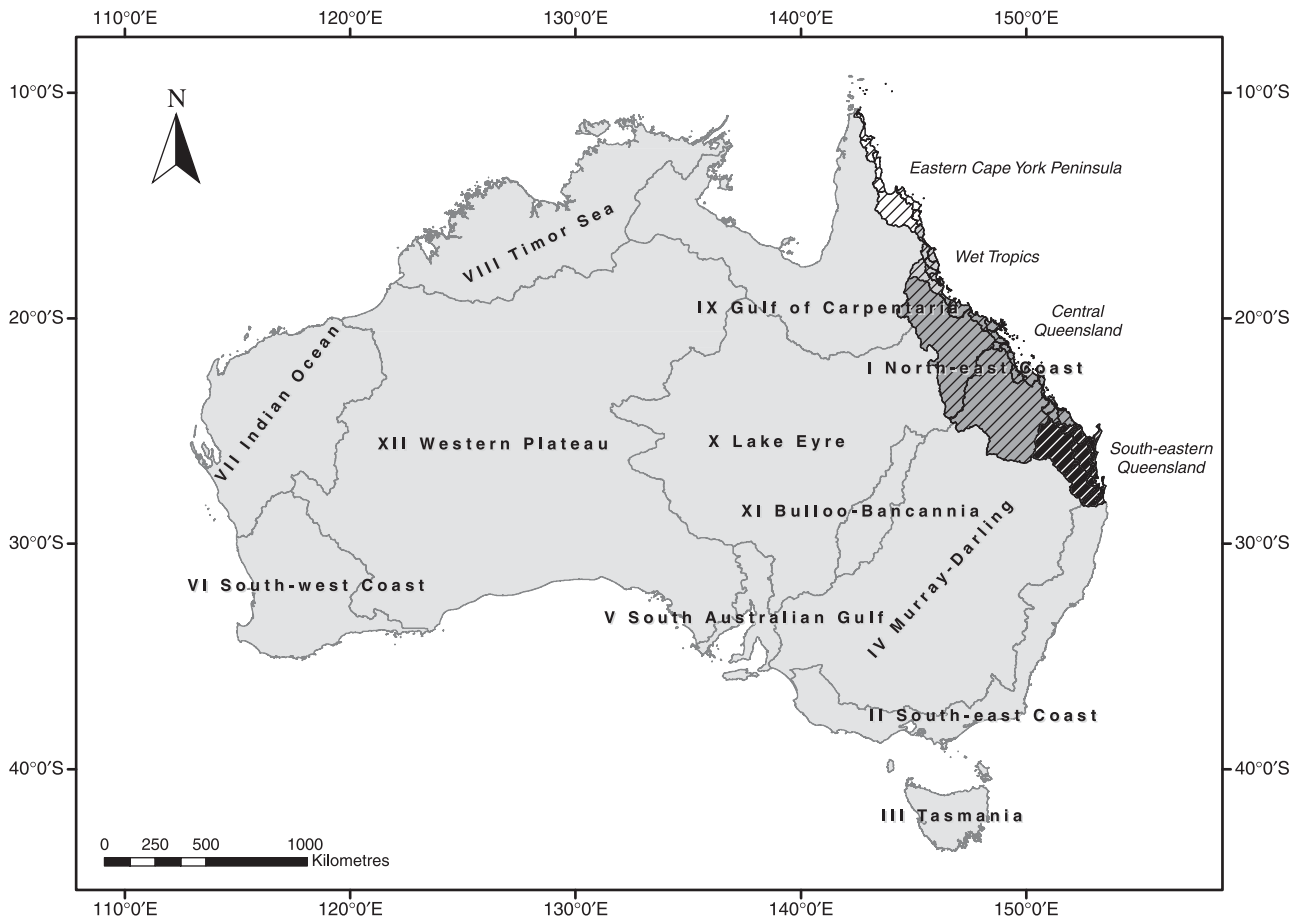
Figure 1 Map of the 12 primary drainage divisions of Australia (Roman numerals) and the four regions of the North-east Coast Division (hatched shading) including eastern Cape York Peninsula ($n = 15$ basins), Wet Tropics ($n = 12$ basins), central Queensland ($n = 11$ basins), and south-eastern Queensland ($n = 15$ basins).

METHODS

Geographical setting

We examined the historical and present-day biogeography of freshwater fishes for 12 primary drainage divisions of Australia, and for 53 basins within four regions of north-eastern Australia (Fig. 1). The Australian Water Resources Commission (1976) defined drainage divisions based largely on landform, climate and the distribution of aquatic habitat types. Although some of the watershed boundaries can be disputed, e.g. the distinction between drainage divisions I and II, the biogeography of Australia's native freshwater fishes strongly reflects these divisions (Unmack, 2001; Allen *et al.*, 2003).

North-eastern Australia comprises a single drainage division that is situated between the Great Dividing Range to the west and the Coral Sea to the east. Although this drainage division represents only *c.* 6% of the continental area, its rivers discharge almost 25% of the total annual discharge for Australia (Pusey *et al.*, 2004). The North-east Coast Division exhibits an enormous diversity of climate, flow regimes, landform and river types across a latitudinal gradient that spans more than 18°. On the

basis of these physical features, this division can be subdivided into four regions (Fig. 1) each containing a number of basins and sub-basins (after Pusey *et al.*, 2004) for which we collated fish species composition data: eastern Cape York Peninsula ($n = 15$), Wet Tropics ($n = 12$), central Queensland ($n = 11$) and south-eastern Queensland ($n = 15$). Similar to the major drainage divisions, these four regions of the North-east Coast Division also differ in their native fish species composition (Unmack, 2001; Pusey *et al.*, 2004).

Fish species data bases

We assembled present-day species lists of native and non-indigenous freshwater fishes. Fish species occurring in natural waterways (i.e. excluding artificial impoundments such as farm ponds or reservoirs associated with water treatment plants) were tabulated for the 12 major drainage divisions using information from Unmack (2001), Allen *et al.* (2003), Burrows (2004), Hammer & Walker (2004), Koehn & MacKenzie (2004), Lintermans (2004), Morgan & Gill (2004), Morgan *et al.* (2004) and Pusey *et al.* (2004). Following Allen *et al.* (2003), we defined a freshwater fish in a relatively broad sense to include those species that can

reproduce in freshwater and diadromous species that spend the majority of their lives in freshwater. We excluded numerous species with strong marine or estuarine affinities that may enter freshwater for only short periods of time. A total of 214 native species and 27 alien fish species (species introduced from other countries that have established self-sustaining populations) were included in the analyses based on these criteria. Of these native species, seven were classified as critically endangered, 12 as endangered and 18 as vulnerable according to a recent listing by the Australian Society for Fish Biology (2004).

Distribution data for freshwater fish species were assembled for each of the 53 basins within the four regions of the North-east Coast Drainage Division using information from Pusey *et al.* (2004) and references therein. A total of 95 native species and 22 alien species were reported. For each basin, we assigned species to the following categories: *native* species are indigenous to a given basin in Australia; *translocated native* species are those that have been translocated to a given basin for which they are not indigenous or in the case of diadromous species that have been (and continue to be) stocked above large dams; *alien* species are those that have been introduced from other countries outside Australia. For the latter two categories we divided the species into those confirmed to have formed self-sustaining populations and those whose successful establishment is still unconfirmed.

We excluded from our data base those species and subspecies that have been translocated and/or stocked to or within basins where they are historically native. For example, this includes recreational species such as sooty grunter, *Hephaestus fuliginosus*, and barramundi, *Lates calcarifer*, that are the subject of ongoing stocking programmes throughout their native ranges, and southern Australian subspecies of eel-tailed catfish, *Tandanus tandanus*, and Murray cod, *Maccullochella peelii*, that have been translocated to rivers within the North-east Coast Division where different subspecies naturally occur. Comparatively few freshwater fish surveys have been undertaken in several river basins (including the Haughton, Don, Proserpine, O'Connell, Plane and Styx basins) and so comprehensive lists of species composition are not available. These river basins were excluded from our data base, as were river basins occurring on coastal islands. We also excluded several species that are likely to have been undersampled and therefore their natural distributions are not well understood in Queensland freshwaters. For all other basins and species, our final data base accurately reflects the current state of knowledge of the distribution of each freshwater fish species within the North-east Coast Drainage Division (Pusey *et al.*, 2004).

Indicators of anthropogenic disturbance

Non-indigenous fish species have commonly been documented to thrive in degraded aquatic habitats (Kennard *et al.*, 2005). We characterized the potential sources and intensity of anthropogenic disturbance in each Australian drainage division using the method and data described in Stein *et al.* (2002). The method uses geographical data recording the extent and intensity of human activities known to impact upon river condition to quantify disturbance for individual stream sections along a continuum from near-pristine to severely disturbed. We computed six major factors of catchment disturbance with potential to significantly alter river processes: (1) land-use activity; (2) settlements and structures; (3) infrastructure; (4) extractive industries and other point sources of pollution; (5) a composite catchment disturbance index (CDI) integrating the previous four indicators; and (6) a flow regime disturbance index (FRDI) reflecting direct alterations to the flow regime from impoundments, flow diversions or discharges and levee banks. These six factors reflect both the spatial extent and potential magnitude of impact from human disturbance.

For each of the disturbance factors, a rating is derived for every stream section based initially only on disturbances to that section or within its immediate subcatchment. For each stream section, a contributing catchment area is determined from a digital elevation model (250 m resolution). Mean disturbance factors and indices for each of the 12 drainage divisions were computed as the average of all grid cells in the stream networks comprising all river basins within each division – each stream segment is assigned one score that is attributed to each grid cell that belongs to the segment. Hence the means are weighted by the number of grid cells in a segment, a surrogate for segment length. All factor and composite index scores are standardized (range 0–1), whereby a value at or near 0 is at the undisturbed end of the continuum, while a value at or near 1 is at the severe disturbance end of the continuum. We refer the reader to Stein *et al.* (2002) for a detailed description of the disturbance indices and their derivation.

Statistical analyses

Beta-diversity is defined as the variability in species composition among sampling units for a given area and is quantifiable based on an array of metrics (Koleff *et al.*, 2003). We used fish presence–absence data for historical and present-day species pools to quantify changes in faunal similarity among major Australian drainage divisions and among river basins of north-eastern Australia according to the Sørensen index (Legendre & Legendre, 1998). This index represents the compositional similarity between two sampling units, which ranges between 0 (no species in common) and 100 (all species in common) when expressed as a percentage. We used the Sørensen index, in part, because the complement of this index is equal to the Bray–Curtis index when using presence–absence data (Legendre & Legendre, 1998), which was required for subsequent analyses. Similarity matrices were calculated separately for historical faunas comprising native species before known introductions or extirpations associated with European settlement, and for present-day faunas comprising native and non-indigenous species minus any extirpations (cf. Rahel, 2000; Marchetti *et al.*, 2001; Taylor, 2004). Note that we know of no confirmed extinctions of species at either the scale of drainages or individual basins in the North-east Coast Drainage Division (except for Mary River cod, *Maccullochella peelii mariensis*, in some river basins of south-eastern Queensland); thus corresponding to invasion-only scenarios of Olden & Poff (2003). Changes in pairwise compositional similarity among

drainages/basins, calculated as $\Delta CS = CS_{\text{present-day}} - CS_{\text{historical}}$, indicates either taxonomic homogenization (i.e. positive ΔCS) or taxonomic differentiation (i.e. negative ΔCS) (Olden & Rooney, 2006). We also predicted future changes in beta-diversity associated with anticipated species invasions and extinctions by repeating the above calculation assuming that future unconfirmed alien and translocated native species will establish self-sustaining populations, and native species identified as critically endangered, endangered and vulnerable (Australian Society for Fish Biology, 2004) will be driven to extinction. Analyses were conducted among all Australian primary drainages and among basins within the geologically and climatically distinct regions of north-east Australia: eastern Cape York Peninsula, Wet Tropics, central Queensland, and south-eastern Queensland.

We tested the null hypothesis of no difference in beta-diversity among sampling units (Australian drainages, north-east coastal basins) before and after species introduction using a test for homogeneity of multivariate dispersions (Anderson, 2006). This method is a multivariate analogue to the univariate Levene's test, and is flexible because it can be based on any ecologically relevant dissimilarity measure. Simply, the test computes an F-statistic to compare the average distance from an individual sample to the group centroid defined in the principal coordinate space of a chosen dissimilarity measure (in our case, Bray–Curtis dissimilarity), and then permutes the appropriate least-squares residuals to estimate statistical significance (P value). By conducting a permutation analysis of multivariate dispersions we avoid the problem that individual dissimilarities between pairs of samples are not independent of one another.

To elucidate possible drivers of faunal homogenization/differentiation for Australian drainages we correlated patterns of beta-diversity in species composition with descriptors of human disturbance. Multivariate dispersion, a measure of beta-diversity, was quantified as the mean distance of all drainages to their group centroid (Anderson *et al.*, 2006). Therefore, changes in compositional similarity with time are calculated as the difference between the distance of each drainage from their group centroid between historical and present-day fish faunas. A positive value indicates that a drainage has shifted closer to the group centroid in multivariate space over time, thus representing taxonomic homogenization (the opposite would represent differentiation). We conducted correlation analyses and multiple linear regression (bootstrap model selection, critical $\alpha = 0.05$: Olden & Jackson, 2000) to relate change in fish compositional similarity to individual disturbance factors and the whole suite of disturbance factors (with the exception of CDI), respectively. A Mantel test was performed to calculate the matrix correlation between changes in compositional similarity and geographical distance between drainages (measured from their centre).

RESULTS

Drainage divisions of Australia

Introductions of alien species have significantly changed the present-day biogeography of Australia's fish faunas by increasing the compositional similarity of drainages with time. The average pairwise change in faunal similarity among drainages was an increase of 3.0%, rising from a historical similarity of 17.1% to a present-day similarity of 20.1%. Changes in compositional similarity have been highly variable across drainages of Australia (Fig. 2). In general, southern Australia (drainage divisions II to VI and ignoring the highly xeric division XII) exhibited greater change (> 4% increase in similarity) than did basins within northern Australia (< 4%). The South-west Coast exhibited the greatest mean percentage increase of 8.4%, followed by the South Australian Gulf (6.7%), Tasmania (6.1%) and the Murray–Darling (4.8%). The widespread introduction of goldfish, *Carassius auratus*, mosquitofish, *Gambusia holbrooki*, common carp, rainbow trout, *Oncorhynchus mykiss*, Eurasian perch, *Perca fluviatilis*, guppy, *Poecilia reticulata*, and brown trout, *Salmo trutta* (in decreasing order of prevalence), have contributed greatly to the homogenization of drainage faunas.

In contrast to the rest of the Australia, Bulloo–Bancannia and Western Plateau showed slight differentiation with the other drainages (average of −1.5% and −1.3%, respectively); an outcome of these drainages having no species introductions. Patterns of differentiation among the remaining pairs of drainages (Table 1) are the result of alien species with restricted distributions, including African cichlids (*Haplochromis burtoni*, *Hemichromis bimaculatus*), South and Central American cichlids (*Amphilophus citrinellus*, *Astronotus ocellatus*, *Cichlasoma octofasciatum*) and an Asian goby (*Acanthogobius flavimanus*) and gourami (*Trichogaster trichopterus*). A comparison of multivariate dispersion between historical and present-day fish faunas supports a change in drainage compositional similarity associated with species invasions (Table 2). Present-day faunal similarity among drainages exhibited smaller, though not statistically significant, multivariate dispersion in ordination space (defined by the principal coordinate analysis) compared with historical faunas.

The majority of the changes in similarity among pairs of drainages were positive (50 out of 66 comparisons or 76%), indicating that fish faunas have become predominantly homogenized in response to species invasions over the 20th century (Fig. 3a). The greatest percentage increase in similarity occurred between the South-west Coast and South Australian Gulf, where the Sørensen index nearly tripled from a historical 16.7% to a present-day 41.0% ($\Delta CS = 24.3\%$). Other extreme examples include the dramatic homogenization of the South-west Coast and Tasmania from a similarity of 16.7% to 34.6% ($\Delta CS = 17.1\%$), and the increase in similarity from 8.5% to 24.6% ($\Delta CS = 16.1\%$) between the Murray–Darling and South-west Coast (Fig. 3b). Notably, the 17 pairs of drainages that historically had zero compositional similarity (i.e. no species in common) now have an average similarity of 2.1%. For instance, the invasion of common carp and mosquitofish to the Lake Eyre and the South-west Coast drainages has resulted in a shift from a historical similarity of 0% to a present-day similarity of 7.3%. In another example, the establishment of nine non-indigenous species into a historical species pool of only nine shared native species has caused a 15.1% increase in similarity between the Tasmania and Murray-Darling drainages. The greatest faunal differentiation
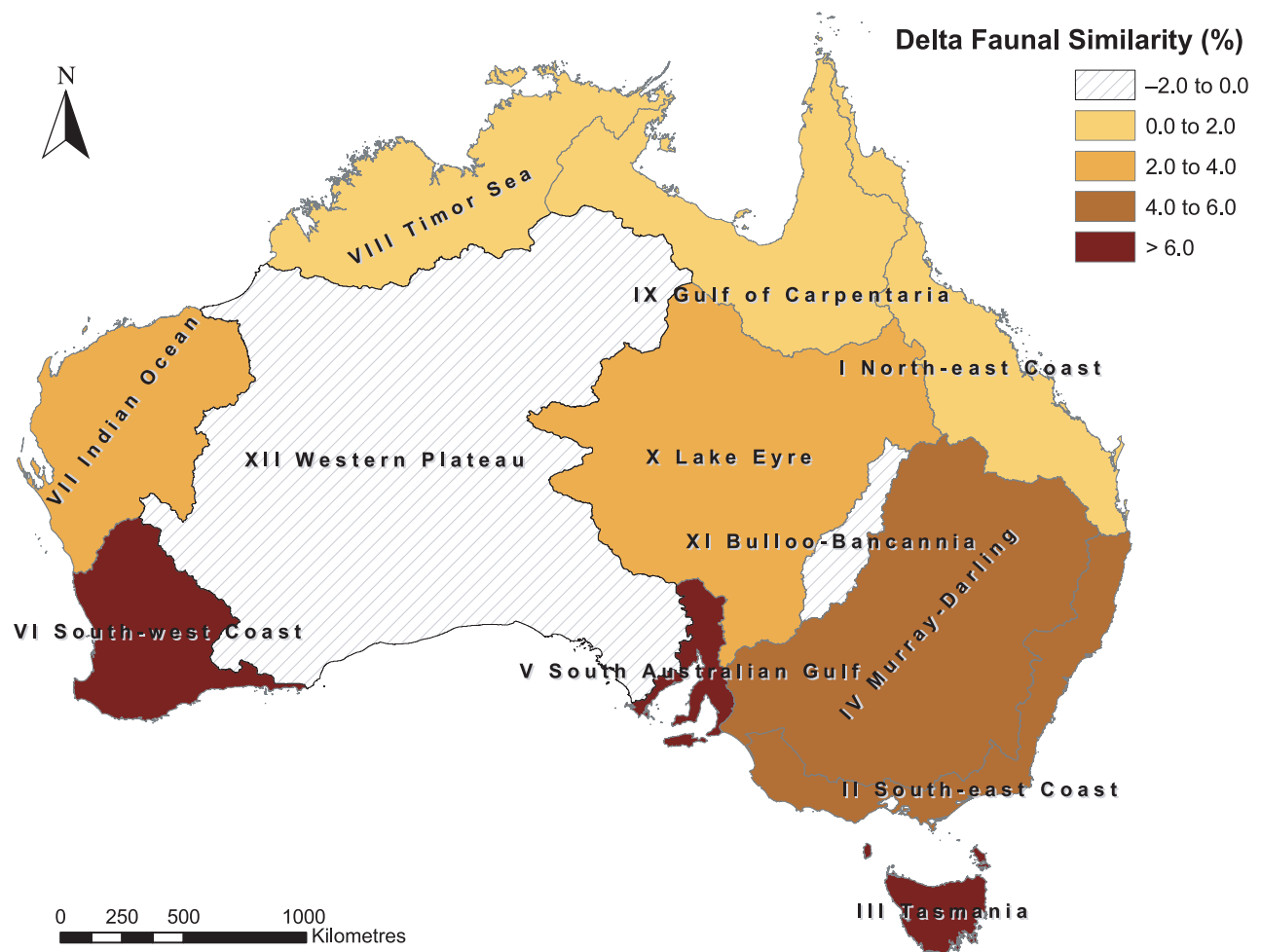
Figure 2 Geographical patterns of percentage change in fish faunal similarity among drainage divisions of Australia before and after human-mediated introduction of non-indigenous species. On average, the compositional similarity among drainages homogenized over time, increasing from a historical similarity of 17.1% to a present-day similarity of 20.1%. See Table 1 for pairwise changes in faunal similarity between drainages.

Table 1 Summary statistics for the 12 primary drainage divisions of Australia. Reported values include the number of native (N) and alien (A) fish species, average change in composition similarity between historical and present-day fish faunas ($\overline{\Delta CS}$), and the pairwise change in composition similarity between drainage divisions based on Sørensen's index. Positive values indicate taxonomic homogenization and negative values indicate taxonomic differentiation.

Drainage divisions		No. species			Change in compositional similarity (ΔCS)											
		N	A	$\overline{\Delta CS}$	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
I	North-east Coast	93	16	1.2												
II	South-east Coast	43	20	4.7	2.5											
III	Tasmania	24	9	6.1	3.0	6.1										
IV	Murray–Darling	35	11	4.8	0.8	7.1	15.1									
V	South Australian Gulf	12	8	6.7	4.8	7.0	12.2	10.8								
VI	South-west Coast	12	7	8.4	4.3	13.5	17.9	16.1	24.4							
VII	Indian Ocean	18	4	2.1	3.1	4.3	3.6	0.4	4.8	4.9						
VIII	Timor Sea	81	4	1.5	−0.6	4.4	1.7	0.7	1.9	1.9	3.6					
IX	Gulf of Carpentaria	71	2	0.6	−3.7	1.2	1.7	0.9	2.2	2.2	2.6	0.0				
X	Lake Eyre	32	4	2.7	2.9	6.8	5.8	0.0	6.2	7.3	4.1	3.9	0.8			
XI	Bulloo–Bancannia	10	0	−1.5	−1.8	−1.0	0.0	−5.2	0.0	0.0	−3.6	−0.4	−0.3	−4.1		
XII	Western Plateau	9	0	−1.3	−1.6	0.0	0.0	−2.7	0.0	0.0	−4.8	−0.7	−0.5	−3.9	0.0	

Table 2 Results from the test of multivariate homogeneity comparing multivariate dispersion of historical and present-day fish faunas. Multivariate dispersion, a measure of beta-diversity, is calculated as the mean distance of all drainages/basins to their group centroid in principal coordinate space defined by Bray–Curtis compositional dissimilarity.

	Multivariate dispersion			
Scale of investigation	Historical	Present-day	F	P
Australian Drainage Divisions	57.06	55.27	0.651	0.43
North-east Division Basins				
Eastern Cape York Peninsula	24.13	24.13	–	–
Wet Tropics	21.52	23.04	0.232	0.63
Central Queensland	17.75	19.61	0.707	0.41
South-eastern Queensland	17.45	18.22	0.113	0.74
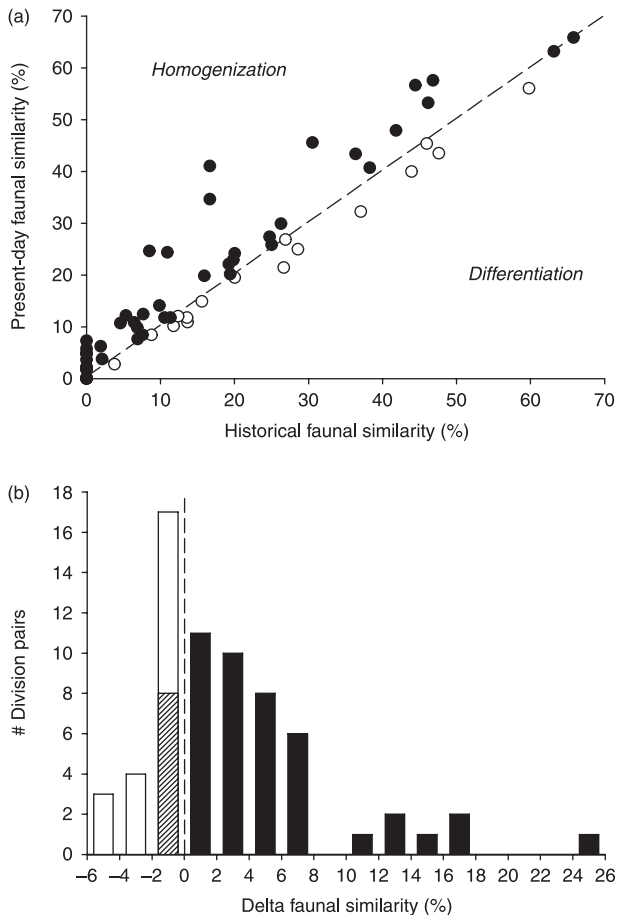
Figure 3 (a) Present-day versus historical compositional similarity for pairwise comparisons ($n = 65$) among the 12 Australian drainages. Filled symbols located above the 1:1 line of equality indicate drainage pairs for which similarity of fish species composition has increased with time (i.e. taxonomic homogenization), and empty symbols located below the 1:1 line indicate drainage pairs for which similarity of fish species composition has decreased with time (i.e. taxonomic differentiation). (b) Frequency histogram of changes in pairwise compositional similarity (ΔCS) among Australian drainages. Change was measured as present-day similarity minus historical similarity, where positive values indicate taxonomic homogenization (filled bars), zero indicates no change (hatched bar) and negative values indicate taxonomic differentiation (empty bars). Evidence for overall fish faunal homogenization with time was supported by the majority of points occurring above the 1:1 line in (a) and to the right of the line or positive values in (b).

was observed for Murray–Darling and Bulloo–Bancannia drainage, which showed a 5.2% decrease in compositional similarity owing to only six shared native species and the unshared invasion of 11 alien species into the Murray–Darling drainage.

Change in beta-diversity as measured by multivariate dispersion was highly correlated with change in compositional similarity (ΔCS) as measured by Sørensen similarity ($R = 0.99$, $P < 0.001$), therefore we used ΔCS as a measure of faunal homogenization in all subsequent analyses. Our results show that the magnitude of faunal homogenization was highest in drainage divisions subjected to the greatest degree of human disturbance. We found a consistent positive association between ΔCS and all disturbance factors, indicating that drainages more impacted upon by human activities have experienced greater faunal homogenization (Fig. 4). Significant relationships were observed for the degree of disturbance associated with CDI ($R = 0.72$, $P = 0.008$; Fig. 4a), land use ($R = 0.69$, $P = 0.010$; Fig. 4b), human settlement ($R = 0.78$, $P = 0.003$; Fig. 4c) and infrastructure ($R = 0.58$, $P = 0.05$; Fig. 4c). The final multiple regression according to bootstrap model selection indicated a strong relationship between ΔCS and human settlement, infrastructure and land use ($R = 0.88$, $F_{3,8} = 8.99$, $P = 0.006$).

Changes in compositional similarity showed no relationship with geographical distance between drainages (Mantel test, $R = 0.02$, permutation $P = 0.41$). This was best illustrated by the fact that the South-west Coast exhibited the greatest homogenization with the distant drainages of South Australian Gulf, Tasmania, Murray–Darling and South-east Coast, whereas it showed no change (i.e. continued to have no species in common) with neighbouring Western Plateau and only small percentage increases with the Indian Ocean and Timor Sea drainages (Table 1). We found a positive logarithmic relationship between change in compositional similarity and percentage change in species richness ($R = 0.94$, $F_{1,10} = 73.2$, $P < 0.0001$), indicating that species introductions are increasing regional or gamma-diversity but decreasing species turnover or beta-diversity.

Coastal basins of north-east Australia

Introductions of alien species have significantly changed the present-day fish biogeography of north-eastern Australia. The average pairwise change in compositional similarity within regions either decreased (central Queensland, –2.8%; Wet Tropics, –2.3%; south-eastern Queensland, –1.6%) or showed no change
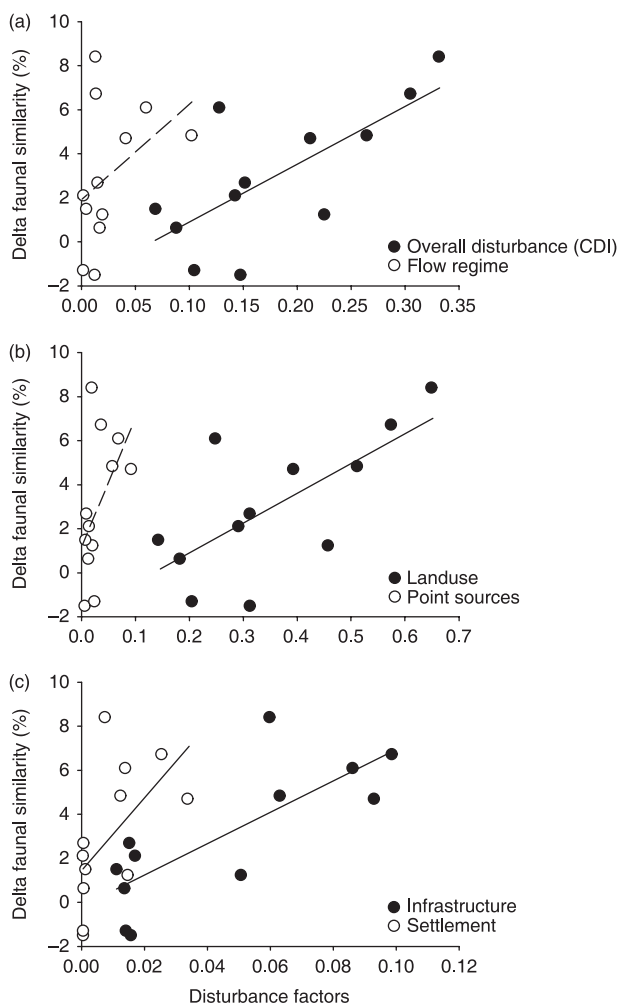
Figure 4 Relationships between delta faunal similarity (%) and disturbance factors reflecting overall disturbance and flow regime (a), land use and point sources (b), and human infrastructure and settlement (c). Solid regressions lines are significant at $P < 0.05$ and dashed lines indicate a non-significant relationship. Faunal homogenization was highest in drainages subjected to the greatest degree of disturbance associated with human settlement, infrastructure, land-use change and overall drainage disturbance.

(eastern Cape York Peninsula), indicating a general tendency towards faunal differentiation. The greatest average decrease in similarity was observed for river basins containing major urban centres, including the Ross River (−8.0%, Townsville), Barron River (−3.8%, Cairns), Logan–Albert rivers (−3.1%, Brisbane) and Fitzroy River (−2.8%, Rockhampton). In contrast, basins exhibiting the lowest levels of differentiation included the comparatively undisturbed areas of the eastern Cape York Peninsula (0%), Maroochy River (−0.44%), Mary River (−1.1%) and Murray River (−1.5%) in the Wet Tropics region of north-eastern Australia. The degree of multivariate dispersion was greater for present-day versus historical fish faunas for all regions, thus supporting the overall observation of taxonomic differentiation, although these differences were not statistically significant (Table 2).
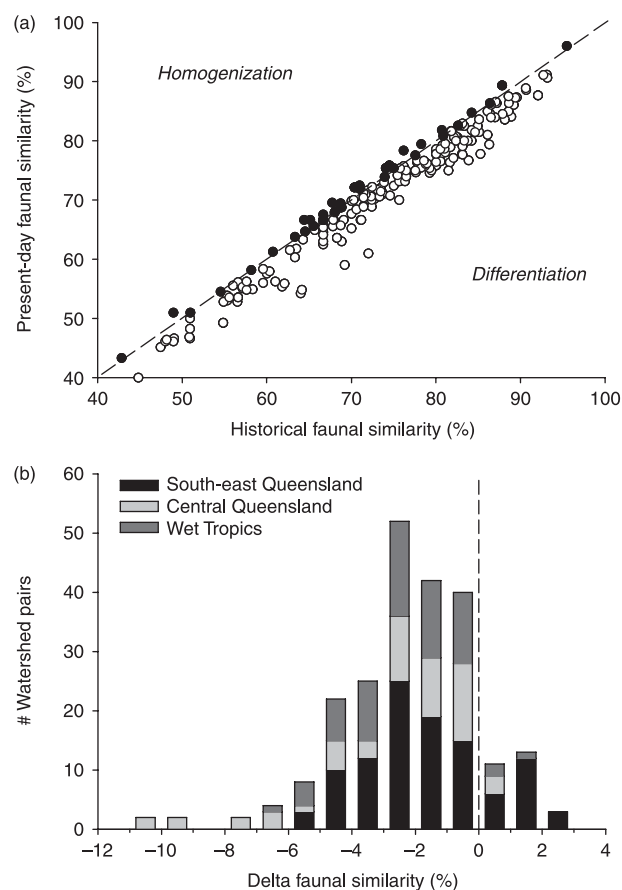

Figure 5 (a) Present-day versus historical compositional similarity for pairwise comparisons among coastal basins within three regions of the North-east Drainage Division (basins in eastern Cape York Peninsula exhibited no change in compositional similarity and therefore are not shown). Filled symbols located above the 1:1 line of equality indicate basin pairs for which similarity of fish species composition has increased with time (i.e. taxonomic homogenization), and empty symbols located below the 1:1 line indicate basin pairs for which similarity of fish species composition has decreased with time (i.e. taxonomic differentiation). (b) Frequency histogram of changes in pairwise compositional similarity (ΔCS) among coastal basins within regions. Change was measured as present-day similarity minus historical similarity, where positive values indicate taxonomic homogenization (filled bars), zero indicates no change (hatched bars) and negative values indicate taxonomic differentiation (empty bars). Evidence for overall fish faunal differentiation with time was supported by the majority of points occurring below the 1:1 line in (a) and to the left of the line or negative values in (b).

The majority of the changes in similarity among pairs of basins were either negative (185 out of 331 comparisons or 56%) or zero (119 out of 331 or 36%) (Fig. 5a). Basins of south-east Queensland exhibited the greatest tendency towards homogenization (22% of pair-wise comparisons), whereas the majority of basins in central Queensland and the Wet Tropics showed a decrease in compositional similarity with time (Fig. 5b). Faunal differentiation was the result of variable patterns of invasion and

a high degree of historical compositional similarity among basins (Sørensen similarity ranged between 42.9% and 95.5%; Fig. 5a). On average, basins have gained three non-indigenous species (alien = 1.83, translocated native = 1.23); a value caused in large part by the addition of more than five species to a set of only 10 basins. Mosquitofish ($n = 24$ basins), platy, *Xiphophorus maculatus* ($n = 16$), guppy ($n = 14$) and swordtail, *Xiphophorus helleri* ($n = 13$), were the most widespread alien species, contributing to the homogenization of basins. However, the sporadic establishment of numerous species, including cichlids (*Amphilophus citrinellus*, *Haplochromis burtoni*, *Hemichromis bimaculatus*, *Tilapia mariae*), oriental weatherloach, *Misgurnus anguillicaudatus*, and *Trichogaster trichopterus*, outweighed the number of these cosmopolitan species and were responsible for patterns of differentiation. In contrast to Australian drainage divisions, change in compositional similarity was negatively associated with percentage change in species richness for central Queensland ($R = 0.86$, $P < 0.001$) and the Wet Tropics ($R = 0.55$, $P = 0.06$), but not for south-east Queensland ($R = 0.03$, $P = 0.91$).

Forecasting future changes in fish biogeography

Assuming that unconfirmed alien and translocated native species will establish self-sustaining populations, and at-risk native species will be driven to extinction in the future, our study predicts that primary drainages of Australia will continue to exhibit taxonomic homogenization, increasing from a present-day similarity of 20.1% to a future similarity of 22.3%. This represents an average increase in compositional similarity of 2.2% from present-day faunas and 5.1% from historical faunas. Likewise, basins of the Wet Tropics are predicted to show a 0.2% increase in faunal similarity compared with the present day (66.7% to 66.9%). In contrast, south-east Queensland (−0.2%; present day 73.9%, future 73.7%), central Queensland (−0.7%; present day 71.2%, future 70.5%) and eastern Cape York Peninsula (−0.2%; present day 65.2%, future 65.0%), are predicted to continue to differentiate, although at a lower rate compared with past changes to the species pool.

DISCUSSION

The changing biogeography of Australian freshwater fishes

The historical biogeography of Australian freshwater fishes, including patterns of species richness and endemism, is well documented in the literature (Unmack, 2001). A long period of isolation of the Australian continent coupled with previous fluctuating aridity and climatic variability have ensured that the fish fauna is highly distinctive and relatively species poor, particularly for primary freshwater species (Allen *et al.*, 2003). Historical climate change and periodic and extensive marine flooding have undoubtedly resulted in widespread extinctions in the past, however these events have been somewhat counterbalanced by extensive colonization and speciation of ostensibly marine groups such as the Atherinidae, Terapontidae and

Plotosidae, particularly in drainages of northern Australia. The generally low relief of the Australian continent and consequent absence of significant barriers to movement has been suggested to have contributed to the evolution of widespread distributions in many species and increased levels of historical similarity between regions (Unmack, 2001; Allen *et al.*, 2003). Nonetheless, barriers imposed by the Great Dividing Range and wide expanses of poorly watered xeric areas (e.g. the Western Plateau) represent a significant determinant of dissimilarity between regions and have been implicated in the evolution of a wide array of sister species and subspecies (Pusey *et al.*, 2004).

Human-aided introduction of alien species and the intentional translocation of native species have a long history in Australia (Arthington, 1991). Our study illustrates the consequences of these invasions for the present-day biogeography of the freshwater fish fauna. Alien fish species were first brought to Australia within a century of European colonization with four cyprinid, one percid and three salmonid species being deliberately introduced between 1850 and 1900 (Koehn & McKenzie, 2004; Lintermans, 2004). These introductions were essentially limited to southern Australia under the auspices of various acclimatization societies so as to allow for more distinguished fishing pursuits than the native fauna was perceived to offer and to reduce the unfamiliarity of the newly colonized country. The number of established alien species increased rapidly from 10 species in the 1950s to more than 30 species by the turn of the millennium, with the great majority of these additional species being derived from species imported for the aquarium hobbyist trade (Lintermans, 2004). The mechanisms by which native fishes have been translocated across Australia vary greatly. At least 49 species of native fishes have been translocated between and within Australian basins to satisfy recreational, aquaculture and conservation outcomes (Lintermans, 2004). In addition, the route of invasion of some native species has included inadvertent exchange in water transfer systems, contamination of stocks for enhancement of recreational fishing and use of native fishes as bait. In some areas, native translocation has been vigorously pursued. For example, 38 species, not all of which have established, have been translocated between or within basins in the Wet Tropics region of north-eastern Australia (Burrows, 2004).

We found clear evidence for the homogenization of fish fauna among drainage divisions of Australia in response to human-mediated species introductions. Fish compositional similarity among drainages has increased by 3.0%, rising from a historical similarity of 17.1% to a present-day similarity of 20.1%, and in some cases the degree of faunal similarity between drainages doubled or even tripled with time. Our study represents the first investigation of continental-scale fish homogenization outside North America, and thus provides an opportunity to compare patterns of change in beta-diversity among regions with very different invasion histories and contrasting environments. We found that the overall degree of fish faunal homogenization for Australia (1.9%) was intermediate between the 1.2% reported for provinces of Canada (Taylor, 2004) and the 7.2% observed for the United States (Rahel, 2000) (all values reported as Jaccard's index of similarity). Faunal homogenization in Australia has

resulted from the widespread introduction and subsequent escape/spread of fishes for recreation (rainbow trout), aquaculture (common carp) and mosquito control (mosquitofish), and from the ornamental/aquarium trade (goldfish, guppy). These fishes are among the most widely introduced species across the globe (Ruesink, 2005), and are responsible for patterns of homogenization observed in different countries (Rahel, 2000; Clavero & García-Berthou, 2006). The remarkable degree of similarity in continental-scale homogenization between the Northern and Southern Hemispheres suggests that homogenization of fish fauna may be ubiquitous across the world. Over the past century, the number of non-indigenous species established in drainages of Australia has greatly outstripped the rate at which native species have gone extinct. That is not to say that introductions have not resulted in species extinctions when viewed at smaller scales (e.g. Barlow *et al.*, 1987). Our results, however, show a strong positive relationship between percentage change in species richness and the degree of taxonomic homogenization for Australian fishes; a result also reported for fish faunas of Canada and the United States (Olden, 2006). This suggests that species invasions are enriching regional species pools but at the expense of losing regional variability or beta-diversity.

Geographical patterns of drainage homogenization were highly concordant with levels of disturbance associated with human settlement, infrastructure and land use. Human settlement directly increases the likelihood of introduction (e.g. due to intentional aquarium releases or accidental escapees from artificial ponds), and disturbance associated with physical infrastructure and land-use change promotes the establishment of alien species by disrupting environmental conditions. Although many factors have potential to influence the likelihood of successful establishment, it has been widely reported that alien fish species are more likely to be introduced in urbanized areas and possess life-history attributes enabling them to persist in degraded environments (Alcaraz *et al.*, 2005; Kennard *et al.*, 2005; Olden *et al.*, 2006). This finding agrees with recent, but still limited, evidence across taxonomic groups that points to the importance of urbanization in driving fish homogenization. For example, Marchetti *et al.* (2001) observed that measures of human occupancy and habitat alteration, including the density of dams and aqueducts in the watershed, were associated with the homogenization of the fish fauna of zoogeographic provinces in California, USA. However, at a smaller spatial scale, Marchetti *et al.* (2006) found that differentiation of the fish fauna for Californian basins was positively correlated with urbanization. We found a similar pattern in north-eastern Australia, where river basins containing major urban centres appeared to show the highest differentiation. Lastly, no relationship was observed between faunal homogenization and geographical distance between drainages; a pattern commonly reported for plant communities (e.g. McKinney, 2004; Qian & Ricklefs, 2006). This result comes as no surprise, given that distance between drainages is a poor descriptor of the climatic and geological factors responsible for the historical biogeography of freshwater systems or the anthropogenic factors (e.g. patterns of human settlement) that determine alien species distributions.

Recent theoretical investigations have demonstrated the remarkable complexity of the biotic homogenization process, and the absolute importance of the consideration of scale, in interpreting the mechanisms and drivers of changes in beta-diversity with time (Olden & Poff, 2003, 2004; Cassey *et al.*, 2006; Marchetti *et al.*, 2006). Our results suggest that the idiosyncratic nature by which fish species have been introduced (and established) are patterns of compositional change that differ across temporal and spatial scales. This was clearly evident for watersheds in north-eastern Australia where we found a large range of biogeographical responses to species invasions, combining to produce an overall decrease of 1.4% in compositional similarity.

There are three main reasons for this trend towards faunal differentiation in north-eastern Australia. First, the homogenization process is dynamic because patterns of species invasions vary over time in response to natural and human-related factors promoting introduction, establishment and spread across the landscape (Olden, 2006). Introductions of fishes in north-eastern Australia have occurred sporadically across rivers in response to the geography of human settlement and habitat degradation (Kennard *et al.*, 2005), resulting in the addition of new species that contribute to faunal differentiation. This may represent a transient phase in the changing biogeography of this region if currently established species continue to be introduced and naturally spread among rivers, leading to future homogenization. The dynamic nature of the homogenization process was recently supported by Clavero & García-Berthou (2006), who showed that the fish fauna of the Iberian Peninsula has exhibited phases of differentiation and homogenization over time in response to both newly introduced and previously established alien species. Second, at smaller spatial scales (i.e. grain of investigation) we are more likely to observe the introduction of different species, thus contributing to greater differences in compositional similarity (Olden & Poff, 2003). We found that homogenization among Australian drainages was greater than for watersheds within the single North-east Coastal drainage; a finding also supported by a number of recent multiple scale comparisons (Taylor, 2004; Marchetti *et al.*, 2006). Third, the degree of historical similarity among regions plays an important role in mediating the per capita effects of species invasions on patterns of compositional similarity (Olden & Poff, 2003). Because north-east Australian coastal watersheds on average shared almost three-quarters of their species pools (compared with only 17% for Australian drainages), species invasions that are shared among watersheds will have a much smaller influence on faunal similarity. In summary, patterns of compositional change over time and across different spatial scales will be both variable and particular to different taxonomic groups and different geographical settings.

What is the future of Australian's fish biogeography?

While the historical biogeography of Australia has certainly been altered to some extent by the effects of human colonization and the introduction of non-indigenous fishes, it still persists and continues to set the foundation for large-scale biodiversity patterns. However, will the homogenization trends we identified

continue into the future? In some senses, undoubtedly yes. Our results indicate that further faunal homogenization is likely to occur in the future if those species currently defined as critically endangered, endangered or vulnerable are indeed driven to extinction and unconfirmed alien species are successful in their establishment. Moreover, the rate of homogenization may accelerate in the light of other large-scale forces of environmental change, including likely future urban and agricultural expansion and scenarios of global climate change, which is elsewhere predicted to result in species extinctions (Xenopoulos *et al.*, 2005). For example, many endemic riffle specialists in the Wet Tropics region of north-eastern Australia are suggested to be under threat from reductions in the constancy of rainfall (Pusey *et al.*, 2007). Endemic species, by their very nature, impart distinctiveness to regions and their loss will necessarily result in homogenization. Similarly, species for which distributions are currently limited by low water temperatures (e.g. alien tilapias) may be able to extend their distributional limits into regions in which they have been historically absent under conditions of elevated temperature.

There is little reason to believe that there will not be further homogenization of Australian's freshwater fishes in the future. First, neither the rate at which native and alien species are being legally stocked into Australian freshwaters nor the rate of establishment of new alien species appears to be showing any indication of reduction (Burrows, 2004; Lintermans, 2004). Second, our results clearly show that infrastructural development and settlement are associated with increasing faunal homogenization. Areas currently with only low to moderate levels of homogenization but for which development is either planned or desired (i.e. much of northern Australia) are predicted to experience further loss of distinctiveness. However, human desires for different species (such as those in the aquarium trade) are constantly changing, which will be reflected in the set of species that are purposefully transported around the world and given the chance to become invasive (Padilla & Williams, 2004). Moreover, changes in the direction and magnitude of trade among countries are likely to change the types and rates of species introductions in the future (Perrings *et al.*, 2005). The end result is often an idiosyncratic pattern of species introductions, with a few species making it to almost everywhere and many more making it to only a few new places. In summary, we expect the future biogeography of Australia's freshwater fishes to be a product of asynchronous patterns of species invasions and extinctions, where faunal homogenization is one logical outcome.

Implications for the conservation biogeography of Australian freshwater fishes

Fish invasions are highly non-random with respect to taxonomy and both the geography and history of environmental change (Alcaraz *et al.*, 2005; Olden *et al.*, 2006). Our study illustrates how the antiquity of Australia's freshwater fish fauna has been, and continues to be, threatened by the invasion of alien species and purposeful translocation of native species across the continent. This pattern reflects a global trend by which humans have greatly increased the connectivity of freshwater systems by

dissolving natural biogeographical barriers to fish movement (Rahel, 2007). In light of the increasing degradation of Australia's freshwater ecosystems, recent efforts have emphasized the need for conservation protection in the form of comprehensive, adequate and representative freshwater reserves (Dunn, 2003; Fitzsimons & Robertson, 2005). To date, only about 2% of the 1400 named rivers in Australia are under protection by virtue of them flowing through a few large terrestrial protected areas (Nevill, 2007). Although conservation of entire river basins offers the best chance of protecting aquatic biodiversity (Kingsford *et al.*, 2005), unfortunately many of these protected waters are small streams that are intermittent or ephemeral, or are major river reaches without protection upstream or downstream (Nevill, 2007). These areas are therefore likely to support only a small fraction of the native freshwater fish diversity in Australia. We believe that the selection of freshwater reserves and the success of conservation planning would benefit from a detailed understanding of how species invasions will affect future patterns of fish biogeography.

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