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The importance of ecosystem-based management for conserving aquatic migratory pathways on tropical high islands: a case study from Fiji

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ABSTRACT

1. Tropical, high islands of the Pacific have developed unique freshwater fish faunas that are currently threatened by a range of human activities. This paper documents distinct differences in life history strategies from fish communities found in streams of Fiji compared with fish assemblages in freshwater systems on larger continental land masses. While river systems of northern Australia and Papua New Guinea have a high proportion of freshwater residents, the Fiji fauna is dominated by amphidromous gobiids that migrate across a broad range of habitats throughout their life cycle.

2. The number of amphidromous fish species and the number of all fish species in mid-reaches of Fiji rivers are significantly affected by loss of catchment forest cover and introductions of tilapia (*Oreochromis* spp.). On average, stream networks with established *Oreochromis* spp. populations have 11 fewer species of native fish than do intact systems. The fish that disappear are mostly eleotrid and gobiid taxa, which have important dietary and economic value.

3. Based on the strong links between catchment land clearing, non-native species introductions and loss of migratory pathways for freshwater fish, spatial information was compiled on a national scale to identify priority areas for conservation in Fiji with intact connectivity between forests, hydrologic networks and coral reefs. Areas with high connectivity included remote, largely undeveloped regions of Vanua Levu (Kubulau, Wainunu, Dama, Udu Point, Natewa, Qelewara) and Taveuni, as well as smaller mapping units (Naikorokoro, Sawakasa) of Viti Levu with low density of roads and high relative amounts of mangroves and reefs.

4. These priority areas for conservation can only be effectively protected and managed through cross-sectoral collaboration and ecosystem-based approaches.

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KEY WORDS: amphidromy; land clearing; *Oreochromis*; fish populations; ecosystem-based management; Fiji

INTRODUCTION

Ecosystem coupling across traditionally recognized boundaries is particularly strong in catchment systems. Individuals moving across freshwater-to-marine interfaces to disperse, forage or occupy different ontogenetic niches can substantially alter the properties of adjacent ecosystems (Werner and Gilliam, 1984; Polis *et al.*, 1997). High island, subtropical and tropical systems of both the Pacific and the Caribbean exhibit an unusually high degree of faunal connectivity. In these locales, a high proportion of fish and invertebrates (decapod crustaceans and gastropod molluscs) are diadromous or display facultative movement across marine and freshwater boundaries (McDowall, 2007). The most prevalent type of diadromy in these settings is the distinct life history pattern of amphidromy (Fitzsimons *et al.*, 2002; Keith, 2003; McDowall, 2007).

Amphidromy is characterized by reproduction in fresh water followed by an obligate downstream migration of larvae and period of several months' growth at sea before returning

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*Correspondence to: Aaron P. Jenkins, Wetlands International-Oceania (Fiji Office), c/o University of the South Pacific, Laucala Campus, Suva, Fiji. E-mail: jenkins_a@usp.ac.fj to freshwater habitats as post-larvae (Keith *et al.*, 2008). Amphidromy may be an adaptive life history strategy on high islands characterized by temporal impermanence of streams (Ryan, 1991; McDowall, 1997). Unlike salmonids in temperate systems that respond to chemical cues specific to their natal catchments (Hasler and Scholz, 1983; Dittman and Quinn, 1996), upstream migrations of amphidromous species may be cued by large pulses of fresh water (Delacroix and Champeau, 1992; Fitzsimons *et al.*, 2002) or adult odours (Baker and Hicks, 2003), either of which would indicate viable upstream habitat. These mass migrations of juveniles support locally important, traditional fisheries (McDowall, 1984; Bell, 1999; Berrebi *et al.*, 2005) and it is likely that they provide important seasonal input to local food webs.

Although amphidromy is particularly common on tropical high islands, it is only one of a broad range of life history strategies that require movement across several habitats (Elliott *et al.*, 2007). For example, some, though not all, populations within the family of freshwater eels (Anguillidae) exhibit semelparous catadromy, whereby adults migrate to sea to reproduce and die, while young return to fresh water (Tsukamoto *et al.*, 1998). Many species also move facultatively in response to favourable environmental conditions for foraging or juvenile development. The juveniles of certain marine fish, such as big-eye trevally (*Caranx sexfasciatus*), that reproduce offshore, commonly enter fresh water opportunistically for feeding and growth.

Faunal movements across habitat boundaries can be affected by human disturbance to hydrologic networks, both through flow interruptions and habitat destruction. For example, high dams and water diversions interrupt migratory pathways in Caribbean and Hawaiian streams (Holmquist *et al.*, 1998; Fievet *et al.*, 2001; Fitzsimons *et al.*, 2005), with indirect effects on basal food resources and community assemblages (Greathouse *et al.*, 2006). Meanwhile, habitat destruction can lead to local extinction of species in connected habitats (Mumby *et al.*, 2004; Weijters *et al.*, 2009). Habitat disturbance may also facilitate the spread of non-native fish species (Leprieur *et al.*, 2008). Non-native fish can reduce native diversity and create barriers to migration through predation, competition or by further degrading conditions (e.g. bioturbation during benthic foraging; Starling *et al.*, 2002; Canonico *et al.*, 2005).

In order to quantify the degree of faunal interconnectedness between aquatic habitats, this paper: (a) documents distinct differences in life history strategies from fish communities found in streams on Pacific high islands compared with those inhabiting freshwater habitats on larger continental land masses; (b) tests how the presence of migratory fish in the Fiji Islands is affected in regions with high anthropogenic disturbance from forest clearing and/or non-native species introductions; and (c) hypothesizes that these disturbances create barriers to migration that reduce instream fish diversity, particularly among species that cross multiple habitat types (i.e. from headwaters to nearshore marine areas). Based on this information, spatial data for Fiji are combined into a geographic information system (GIS) to identify priority areas for conservation in Fiji with intact connectivity between terrestrial catchments, hydrologic networks and coral reefs. Lastly, we offer recommendations for preservation of migration pathways through management with ecosystem-based management (EBM) principles.

METHODS

Study region

The Fiji island archipelago, located between 12-22°S and 176°E-178°W, includes 332 islands with a total land area of 18 270 km^2 (Neall and Trewick, 2008). The three largest islands are Viti Levu (10 642 km^2), Vanua Levu (5807 km^2) and Taveuni (437 km^2). The geologic origin of Viti Levu began following convergence of a series of oceanic island-arc fragments (Nunn, 1994). Uplift of plutonic intrusions during the middle to late Miocene (>12 Ma) formed its first significant land mass (Neall and Trewick, 2008), while continuing uplift of central Viti Levu occurred throughout the Quaternary (Nunn, 1994). Vanua Levu formed shortly before 7 Ma and rotated clockwise as the central North Fiji Basin triple junction developed (Kroenke, 1996). Both of these islands have steep slopes and well developed estuaries along coastal floodplains, particularly at the mouths of larger rivers such as the Rewa, Ba, Qawa, Labasa and Dreketi. By contrast, the basaltic, volcanic island of Taveuni is less than 1 Ma, with high grade slopes and few estuaries (Ryan, 1991). Mean annual rainfall is very high in the south-east of Viti Levu and Taveuni and the southern portions of Vanua Levu (>3200 mm, calculated with data from the Fiji Meteorology Service), with largest inputs during the summer cyclone season from November to May. The north-west portions of Viti Levu and Taveuni, together with the northern portions and Natewa Peninsula of Vanua Levu, fall in rain shadows of the ranges and therefore receive lower mean annual rainfall (<2000 mm).

Catchment sampling

Fish communities within 50 m reaches of mid ($n = 20$) and lower sections ($n = 8$) of 20 river basins were sampled between 2002 and 2008 (Figure 1, Table 1). The sites were selected from catchments with a broad range of forest cover (described below), with widespread geographical distribution across Viti Levu, Vanua Levu, and Taveuni. A variety of techniques was used to collect fauna from the rivers/streams to ensure comprehensive presence/absence assessment. These techniques included: electrofishing using either a Deka 3000 (Marsberg, Germany) (600 V, 10 A) or Smith-Root (Vancouver, WA, USA) (500 V, 10 A) backpack unit; netting with gill nets (1 inch mesh), large seine nets (0.4 cm^2 mesh), medium pole seine nets (1 mm^2 mesh) and small hand nets (1 mm^2 mesh); and observations by mask and snorkel. All sites were sampled by 4–6 surveyors working upstream for 1 h per site. Specimens easily identified in the field were released, while those requiring more detailed taxonomic evaluation were collected, fixed in a 10% formalin solution and transferred to 70% ethanol solution after 5 days of fixation. Voucher specimens were deposited in collections at the University of the South Pacific, Suva.

At each sampling site a GPS position and altitude were taken using a Garmin GPS *map* 76Cx. Water quality characteristics were taken before entering the water to minimize disturbance: temperature (°C) and conductivity (μS) readings were taken using a hand-held YSI multi-meter. Brief notes were also taken on riparian vegetation and instream condition with particular emphasis on substrate type, flow type, instream cover, aquatic vegetation, riparian vegetation, land-use type and major disturbance type.

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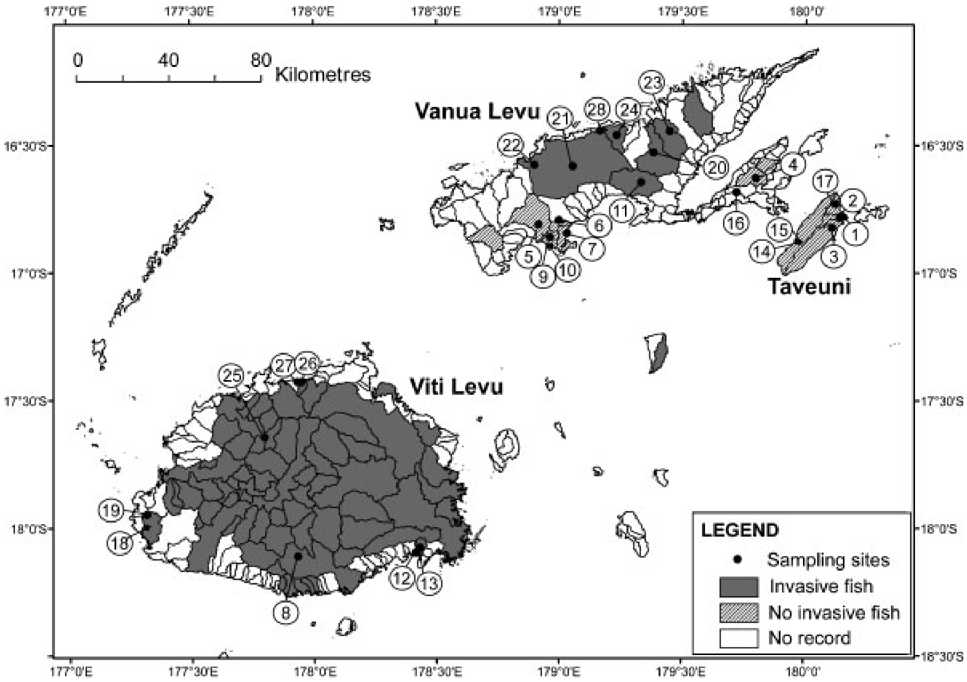

Figure 1. Catchments of Viti Levu, Vanua Levu and Taveuni within the Fiji island archipelago. Dark grey catchments have records of invasive fish in major waterways. Collections of fish from catchments with diagonal bars have no invasive fish. There are no records from open (white) catchments. Dots indicate locations of freshwater sampling sites: 1–Tavoro low; 2–Tavoro mid; 3–Waitavala mid; 4–Buca mid; 5–Wainunu mid; 6–Kilaka mid; 7–Kilaka low; 8–Navua mid; 9–Suetabu mid; 10–Suetabu low; 11–Nasekawa mid; 12–Savura low; 13–Savura mid; 14–Lavena low; 15–Lavena mid; 16–Drekeniwai mid; 17–Navaka mid; 18–Kubuna low; 19–Kubuna mid; 20–Labasa mid; 21–Dreketi mid; 22–Dreketi low; 23–Qawa mid; 24–Tabia mid; 25–Ba mid; 26–Waisai–low; 27–Waisai mid; 28–Macuata-i-wai mid.

Table 1. Freshwater sampling locations from Viti Levu, Vanua Levu and Taveuni (Figure 1)

ID	River/Stream	Mid/Low	Latitude	Longitude	% Forest cover	Dist. upstream (km)	Slope (degrees)	Temp (°C)	Conductivity (μS)	*Oreochromis* spp.
1	Tavoro	Low	16.7833 S	179.8471 W	84	2.48	13.083	25.5	38.4	N
2	Tavoro	mid	16.7824 S	179.8582 W	84	3.85	15.380	23.2	37.2	N
3	Waitavala	mid	16.8264 S	179.8910 W	84	2.36	55.370	26.7	63.5	N
4	Buca	mid	16.6335 S	179.8003 E	84	7.93	30.768	22.5	122.6	N
5	Wainunu	mid	16.8168 S	178.9167 E	80	12.89	19.546	19.4	53.1	N
6	Kilaka	mid	16.8001 S	179.0001 E	80	7.40	15.151	24.5	160.6	N
7	Kilaka	low	16.8501 S	179.0334 E	80	0.16	2.592	27.6	223.4	N
8	Navua	mid	18.1168 S	177.9336 E	80	51.63	35.729	24.6	110.8	Y
9	Suetabu	mid	16.8668 S	178.9642 E	72	9.92	13.299	28.0	290.3	N
10	Suetabu	low	16.9001 S	178.9667 E	72	2.14	10.524	29.0	307.6	N
11	Nasekawa	mid	16.6501 S	179.3334 E	71	16.96	30.550	24.7	107.7	Y
12	Savura	low	18.1003 S	178.4169 E	68	0.87	6.683	26.0	93.0	N
13	Savura	mid	18.0834 S	178.4334 E	68	7.30	21.068	26.8	74.9	N
14	Lavena	low	16.8802 S	179.9673 E	64	1.01	16.908	28.0	46.9	N
15	Lavena	mid	16.8838 5	179.9778 E	64	2.24	19.199	26.1	46.9	N
16	Drekeniwai	mid	16.6881 S	179.7208 E	64	6.60	16.599	24.2	210.7	Y
17	Navaka	mid	16.7331 S	179.8770 W	64	2.08	9.632	27.5	55.0	N
18	Kubuna	low	18.0001 S	177.3168 E	61	8.79	16.762	26.4	302.5	Y
19	Kubuna	mid	17.9501 S	177.3168 E	61	17.34	16.762	25.3	323.5	Y
20	Labasa	mid	16.5334 S	179.3835 E	61	26.88	13.602	24.2	329.0	Y
21	Dreketi	mid	16.5882 S	179.0557 E	57	36.24	13.151	25.2	91.7	Y
22	Dreketi	low	16.5834 S	178.9001 E	57	3.57	6.863	27.0	36.6	N
23	Qawa	mid	16.4502 S	179.4502 E	54	13.86	8.723	26.9	326.0	Y
24	Tabia	mid	16.4667 S	179.2335 E	47	6.37	6.986	27.8	158.4	Y
25	Ba	mid	17.6503 S	177.8002 E	29	40.79	25.180	22.6	117.0	Y
26	Waisai	low	17.4334 S	177.9501 E	1	0.00	0.000	26.8	298.0	Y
27	Waisai	mid	17.4335 S	177.9335 E	1	0.79	8.624	28.2	186.6	Y
28	Macuata-i-wai	mid	16.4487 S	179.1655 E	29	2.63	16.449	25.0	97.5	N

Each record is shown with percentage catchment forest cover, distance upstream (km), maximum downstream slope (degrees), stream temperature (°C), conductivity (μS), and whether or not there were established *Oreochromis* spp. present (Y/N).

Life history classification

A comprehensive list of fish occurring in fresh and brackish waters of the Fiji archipelago was compiled from Jenkins and Boseto (2003), Boseto (2006), and Boseto and Jenkins (2006), plus additional species collected by those authors since 2006. The Fiji freshwater fish fauna for the entire archipelago and for the 20 catchments surveyed for this study were classified according to life history and feeding guild categories for fish largely derived from the classification system of Elliott *et al.* (2007). Feeding guild categories included: generalist; detritivore generalist/specialist; planktivore generalist/specialist; herbivore generalist/specialist; invertivore generalist/specialist; insectivore generalist/specialist; piscivore generalist/specialist; and carnivore. Life history classes included: freshwater resident; freshwater straggler; estuarine migrant; marine migrant; marine straggler; amphidromy; obligate catadromy; and facultative catadromy (Elliot *et al.*, 2007). However, the definition of amphidromy given by McDowall (2007) was used, which appears more appropriate for high island systems. Based on work by Tsukamoto *et al.* (1998), freshwater eels were classified as facultative catadromous, as some anguillid populations have been found to stay within marine systems throughout their lives.

In order to demonstrate the high proportion of high island fish species which occupy multiple habitats throughout their life cycle, the habitat ranges of Fiji fishes were compared with those from larger continental masses on north-eastern Queensland, Australia (Russell *et al.*, 2003) and mainland Papua New Guinea (PNG; Coates, 1993). Fish from each group were classified into six categories based on potential extent of habitat range, assuming no barriers to dispersal or migration: (I) headwaters to marine; (II) mid-reach to marine; (III) low-reach to marine; (IV) estuarine to marine; (V) mid-reach to estuarine; (VI) freshwater only (Figure 2(a)). We tested the hypothesis that the insular fish fauna of Fiji would have a higher proportion of fish with broad habitat ranges, crossing at least four habitat types and including oceanic life history stages.

Statistical analysis of factors to explain species assemblages

Spatial variables (catchment forest cover, distance upstream, maximum downstream slope) that are known to influence freshwater fish assemblage composition (Eikaas and McIntosh, 2006) were collated from remote sensing and GIS data using ArcGIS 9 and MapInfo software. Forest classes from the most recent forest function map for Fiji were combined to form a merged forest layer, which included multiple-use, protection, preservation and hardwood plantation forests at scattered, medium and dense cover (Watling, 1994). The forest function map was originally created by the Fiji Department of Forestry by digitizing

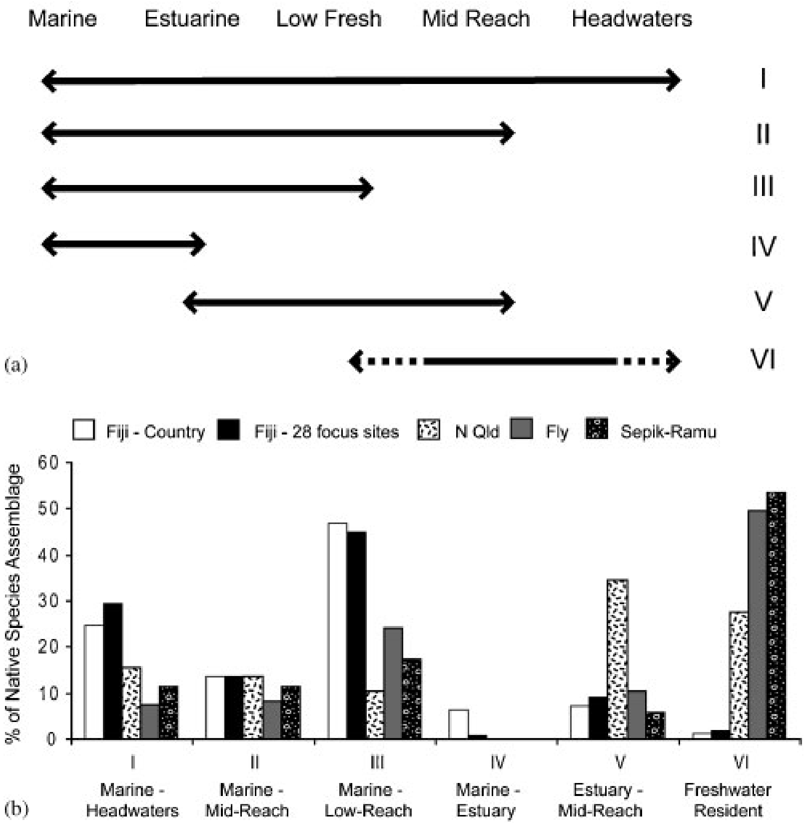

Figure 2. (a) Classification (Groups I–VI) of fish according to the potential extent of habitat range throughout each species life cycle, assuming no barriers to dispersal/migration. (b) Comparison of habitat ranges of fish fauna found in fresh water from Fiji-wide ($n = 154$ species), Fiji 28 focus sites in this study ($n = 104$ species), North-east Queensland ($n = 58$ species, Russell *et al.*, 2003), and the Fly ($n = 145$ species) and Sepik-Ramu ($n = 69$ species) river systems of Papua New Guinea (Coates, 1993).

mosaicked 1991/1992 Landsat satellite data and was verified from field validation data, though no accuracy assessment was produced. Multiple-use forests include natural forests, declared forest reserves and forest areas suitable for regeneration that may be used for production of timber and non-timber forest protects, wildlife habitat, water supply protection and recreation. Protection forests include forests on slopes $>30^\circ$ above 650 m and other erosion prone sites where use is limited to harvesting non-timber forest products. Preservation forests are areas declared reserves for designated water supplies and conservation areas (Sue, 2007).

In order to test the hypothesis that catchment forest cover influences instream fish diversity, particularly of amphidromous fish, percentage forest cover by catchment was determined for Viti Levu, Vanua Levu and Taveuni by intersecting the forest cover class with catchment boundaries. Catchment boundaries were manually digitized following ridges and other obvious geographical features separating draining basins with reference to 25 m digital terrain model (DTM) with contour shading, hydrology network, 20 m relief contours, and scanned and georeferenced Government of Fiji topographic maps (1982–2002) (Atherton *et al*., 2005). Owing to the large number of very small creeks in coastal catchments, creeks were grouped into larger functional catchments containing up to 20 creeks draining into the same embayment or along the same section of coastline (Atherton *et al*., 2005).

To determine if instream fish diversity is also influenced by distance from river mouths and maximum downstream slope, the distance upstream of each freshwater sampling site was calculated based on the length (km) of the hydrologic network from the coastline to the GPS reference point for each site. Shapefiles of rivers and streams from the Fiji Department of Lands were combined to create a unique hydrology layer that was merged with the GPS records of instream survey sites to truncate the waterways to sampling positions. These truncated waterways were used to mask a slope map calculated from the DTM (25 m) for Viti Levu and Vanua Levu. As there was no DTM coverage for Taveuni, a NASA Shuttle Radar Topography Mission (SRTM) 3 arc-second (approximately 90 m horizontal data) digital elevation model (DEM) covering all of Fiji was used for those sites. Maximum downstream slope was determined from the highest value of the pixels downstream from each sampling point.

Both spatial (catchment forest cover, distance upstream, maximum downstream slope) and instream water quality variables (conductivity, temperature) were investigated to explain variance in fish assemblages across the 20 catchment sampling sites. Proportion of forest cover was arcsine square root transformed, distance upstream was $\log_{10}$ transformed, and conductivity was square root transformed to meet assumptions of normality. Akaike's information criterion (AIC) was used to select the best subset of the continuous predictor variables for regression analysis (Quinn and Keough, 2002). Dependent measures of fish community structure included the number of mid-reach amphidromous species, total number of mid-reach fish species, total number of lower-reach fish species, and number of lower-reach euryhaline species. Euryhaline fish species included marine migrants, marine stragglers, and estuarine migrants as defined by Elliott *et al*. (2007). All dependent variables and residuals were normally distributed. Analysis of covariance (ANCOVA) was used to assess the effects of tilapia introductions on numbers of amphidromous and total mid-reach fish species, with significant continuous variables (forest cover and/or distance upstream) added as covariates.

Records of non-native introductions

Records of invasive fish in Fiji were derived from the Fiji Freshwater Fishes Database (A. Jenkins, unpublished data) and introduction records of the Fiji Department of Fisheries from 2006. It is assumed that Fiji Department of Fisheries introductions of Mozambique and Nile tilapia (*Oreochromis mossambicus* and *O. niloticus*) during this time period have all led to established wild populations. All other records are based on direct field observations. The compiled data were overlain on the Fiji catchment map described above.

Priority connectivity regions

In order to place the results into a cross-habitat management context for Fiji, a set of decision rules were used that considered habitat intactness and complexity, hydrology, and sensitivity to erosion to identify regions of Viti Levu, Vanua Levu and Taveuni with high potential for connectivity between terrestrial, freshwater and marine systems. Catchments draining into a single traditional fishing ground (*qoliqoli*) were merged with the *qoliqoli* region to create 76 individual mapping units. In some cases where the boundary between small, adjacent *qoliqoli* occurred within the river mouth, the two *qoliqoli* were combined. Each mapping unit was scored for relative erosion potential, road density, number of creek crossings, presence/absence of non-native freshwater fish, mangrove area relative to catchment size, mangrove habitat complexity, reef area relative to *qoliqoli* size, and reef habitat complexity (Table 2). Mangrove and reef habitats were included because many of the fish found in Fiji's freshwater systems utilize these habitats at varying stages in their life cycles.

The Relative Erosion Potential (REP) index was developed based on environmental factors influencing erosion to determine the relative susceptibility of soil loss from each catchment (Atherton *et al*., 2005). The major determinants of soil erosion are rainfall erosivity and soil erodibility, which are dependent on slope, vegetative cover and level of cultivation (Douglas, 1967). A model of REP, based on the methodology of Watling (1994), was constructed for Fiji catchments with the following equation:

REP = slope factor + land cover factor + rainfall intensity factor + rainfall seasonality factor + soil factor

For Vanua Levu and Taveuni, the REP was calculated with the first three factors only and weighted on a separate scale. Specifications for calculations of each of the above factors are described in detail in Atherton *et al*. (2005).

The density of Fiji's road network serves as proxies both for: (1) the relative level of infrastructure and development; and (2) sources of sediment to catchment streams. The majority of roads are not sealed, often poorly designed and may be constructed on steep slopes with poor drainage. Road density (length in km per km^2 of

Table 2. Decision rules for GIS weightings for mapping priority connectivity regions in Fiji

Factor and Rule	Class	GIS value assigned
Relative Erosion Potential (Viti Levu)	*Proportional averaging across subcatchments*	*Range split into thirds*
7.5–8.9	Low	4
>8.9–10.1	Medium	1
>10.1–11.4	High	–2
Relative Erosion Potential (Vanua Levu + Taveuni)	*Proportional averaging across subcatchments*	*Range split into thirds*
4.3–5	Low	4
>5–5.6	Medium	1
>5.5–6.2	High	–2
Road density (length in km per km^2)		
0-1	Low disturbance	4
>1-2	Moderately disturbed	1
>2 and above	Highly disturbed	–2
Creek crossings (per km^2)		
0–1.5	Low disturbance	4
>1.5–3	Moderately disturbed	1
>3 and above	Highly disturbed	–2
Invasive fish		
No record		0
Invasives present	Highly disturbed	–4
Invasives absent	Intact	6
Mangroves (ha km^{-2})	*Relative to size of catchment*	*Range split into thirds*
0–1.18	Low	0
>1.18–3.45	Medium	1
>3.45–11.3	High	2
Mangrove complexity		
	Fringing mangroves only	
	Mangrove islands or riverine mangroves	+1
	Both mangrove islands and riverine mangroves	+2
Reef (ha)	*Relative to size of qoliqoli (ha)*	
0–0.08	Low	0
>0.08–1.9	Medium	1
>1.9–1.23	High	2
Reef complexity		
	Just fringing	0
	Fringing + patch	+1
	Fringing + patch + outer or reefs around mangrove islands	+2
	Fringing + patch +reefs around mangrove islands + outer or double barrier	+3

catchment area) was calculated from a digital map of Fiji's road network from the Department of Lands intersected with the 76 catchment mapping units. In addition, as creek crossings are specific entry points for sediment washing off roads into creek channels, a count was made of the number of times roads crossed creeks (mapped by the Department of Lands) per km^2 within each mapping unit. Creek crossings may further disrupt flow and connectivity as they often require large fills in natural drainage channels.

Catchments with field or Fisheries Department records of non-native fish introductions (see above) were weighted negatively, while catchments with streams where the absence of invasive fish has been field verified were given strong positive weightings (Table 2). Mangrove area for the main Fiji islands was digitized by the Fiji Department of Forestry from 2001 Landsat ETM+ data. Mapping units were scored based on the extent of mangrove area relative to catchment area and received additional positive weighting for multiple types of mangrove habitats (e.g. riverine and/or mangrove island). Reef area was calculated from total extent of exposed and submerged reefs mapped by the Department of Lands from aerial photographs captured in 1994 and 1996 over Fiji's reefs. Where data were missing, reef area was digitized from Fiji topographic map sheets at 1:50,000 scale. Mapping units were scored based on reef density (reef area relative to the size of *qoliqoli* area). Mapping units received additional positive weightings for multiple types of reef habitats (e.g. fringing, patch and outer barriers or reefs around mangrove islands).

RESULTS

The Barron and Mitchell rivers of north Queensland and the Sepik-Ramu and Fly rivers of Papua New Guinea have a much greater proportion of freshwater residents (Group VI; 27.6%, 49.7% and 53.6%, respectively, for north Queensland, Fly and Sepik rivers) compared with oceanic, high islands such as Fiji (1.3% country-wide; Figure 2(b)). These freshwater residents are largely composed of families represented on the larger continental masses that are completely absent from island fauna. The most speciose of these families include Melanotaenidae, Atherinidae, Pseudomugilidae, Ariidae and Plotosidae. For example, the combined Sepik-Ramu and Fly rivers have highly diverse catfish fauna ($n = 32$ species), among which only two are diadromous. In addition, there are seven species of Terapontidae from PNG, of which only one is diadromous (*Mesopristes argenteus*); this is the only genus from Terapontidae to diversify within the oceanic Pacific islands. North Queensland fish fauna is dominated (34.5%) by species that range between estuaries and mid-reach waterways (Group V). These fish include barramundi (*Lates calcarifer*), two species of sole (Soleidae), and five species of glass perchlets (*Ambassis* spp.) that are not found in Fiji. While the Fly River fauna has a lower proportion of Group V species, there is high representation of apogonids (*Glossamia* spp.) that are not present in Fiji or north Queensland. The freshwater fish fauna in Fiji includes a greater number of species that have oceanic interactions (Groups I–IV). This is due to the high numbers of amphidromous species, particularly through diversification in the gobiid sub-family Sicydiinae (Appendix A).

Factors influencing fish species assemblages

The best-fit model to explain amphidromous fish species number in mid-reach sites included catchment forest cover, distance upstream, and maximum downstream slope. Only catchment forest cover ($P<0.001$) and distance upstream

Table 3. Multiple regression results of best-fit predictor variables on amphidromous fish species number (a) and total fish species number (b) at mid-reach sites. Linear regression results of catchment forest cover on total fish number (c) and euryhaline fish number (d) at low reach sites.

	β	Partial correlation	Tolerance	t	P
a. Mid-reach ampbidromous fish number ($R = 0.848$, *Adjusted* $R^2 = 0.666$, $F_{(3,16)} = 13.613$, $\boldsymbol{p<0.0002}$)					
Catchment forest cover	0.832	0.824	0.859	5.815	**0.0000**
Distance upstream	−0.538	−0.677	0.823	−3.675	**0.0020**
Maximum downstream slope	−0.094	−0.156	0.798	−0.633	0.5358
b. Mid-reach total fish number ($R = 0.754$, *Adjusted* $R^2 = 0.488$, $F_{(3,16)} = 7.030$, $\boldsymbol{p<0.0032}$)					
Catchment forest cover	0.781	0.741	0.859	4.409	**0.0004**
Distance upstream	−0.375	−0.459	0.823	−2.069	0.0551
Maximum downstream slope	−0.141	−0.188	0.798	−0.768	0.4538
c. *Low-reach total fish number* ($R = 0.814$, *Adjusted* $R^2 = 0.606$, $F_{(1,6)} = 11.783$, $\boldsymbol{p<0.0139}$)					
Catchment forest cover	0.814	N/A	N/A	3.433	**0.0139**
d. Low-reach euryhaline fish number ($R = 0.684$, *Adjusted* $R^2 = 0.379$, $F_{(1,6)} = 5.281$, $p = 0.0613$)					
Catchment forest cover	0.684	N/A	N/A	2.298	0.0613

All regression results are reported with correlation coefficient (R), adjusted R^2, F statistic with degrees freedom, and *P* values for the entire model. All significant values are in bold.

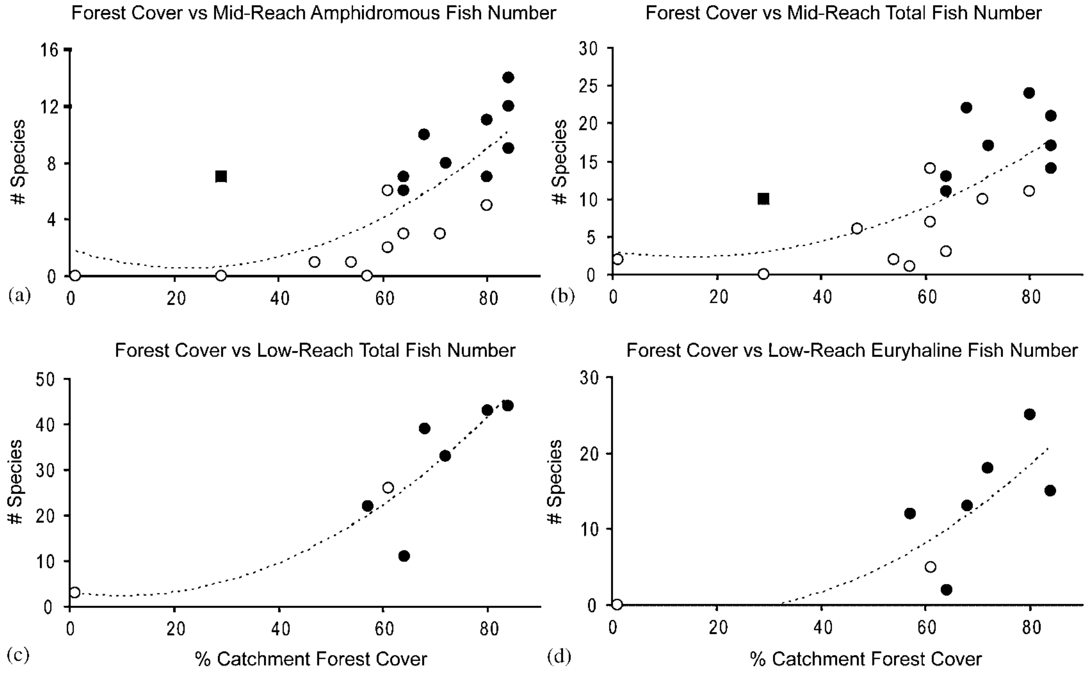

Figure 3. Relationships between catchment forest cover and species number for (a) amphidromous fish in mid-reaches; (b) total fish in mid-reaches; (c) total fish in low-reaches; and (d) euryhaline fish in low-reaches, which includes marine migrants, marine stragglers and estuarine migrants. Solid points are sampling sites without *Oreochromis* spp. while open circles represent sampling sites with *Oreochromis* spp. The rectangle indicates a well-managed catchment (Macuata-i-wai) with prohibition on instream fishing, riparian clearing and dumping of waste.

($P<0.01$) were significant predictors (Table 3(a), Figure 3(a)). When both of these variables were added as covariates to assess effects of *Oreochromis* spp. introductions, only tilapia and catchment forest cover were significant ($P<0.01$; Table 4(a)). On average, mid-reach sites with invasive tilapia had seven fewer species of amphidromous fish (Figure 4(a)). Amphidromous species that were notably absent where *Oreochromis* spp. occurred included the eleotrids *Belobranchus belobranchus*, *Butis amboinensis*, *Giurus hoedti*, and *Ophiocara porocephala*; and the gobiids *Glossogobius* sp.1, *Lentipes kaaea*, *Redigobius bikolanus*, *Sicyopus* (c.f. *Juxtastiphodon*) sp., *Stiphodon rutilaureus*, *Stiphodon* sp. 1, and *Akihito* sp (Appendix A). The gobiids *Redigobius leveri*, *Schismatogobius vitiensis* and *Stiphodon* sp. 2 were also highly sensitive, and were only present in one mid-catchment each where tilapia were recorded.

When total mid-reach fish species number was considered, the best-fit model also included catchment forest cover, distance upstream and maximum downstream slope. Only forest cover was a significant predictor of total species number (Table 3(b), Figure 3(b)). When catchment forest cover and introduced tilapia were considered simultaneously, both factors were significant ($P<0.05$ and $P<0.01$, respectively; Table 4(b)). Mean number of total fish species dropped by 11 in mid-reach sites with *Oreochromis* spp. (Figure 4(b)). While a large number of absent species were the sensitive amphidromous species listed above, they also included *Zenarchopterus dispar*, *Lutjanus argentimaculatus*, and *Microphis brachyurus brachyurus* in low gradient rivers (Appendix A). In addition, *Kuhlia* spp. were not found from mid-catchment sites with tilapia when catchment forest cover was below 60%. Of fish species absent in mid-reach sites with tilapia, five of nine were endemic to Fiji.

Table 4. Analysis of covariance (ANCOVA) of the presence/absence of tilapia plus significant continuous predictor variables from multiple regression analysis on (a) mid-reach amphidromous fish number and (b) mid-reach total fish number. All significant values are in bold

	SS	df	MS	F	p
a. Mid-reach amphidromous fish number					
Catchment forest cover	37.663	1	37.663	9.852	**0.0063**
Distance upstream	6.780	1	6.780	1.774	0.2016
Tilapia	38.896	1	38.896	10.174	**0.0057**
Error	61.168	16	3.823		
b. Mid-reach total fish number					
Catchment forest cover	110.119	1	110.119	5.809	**0.0276**
Tilapia	269.554	1	269.554	14.219	**0.0015**
Error	322.281	17	18.958		

Catchment forest area was significantly related to the total number of fish species recorded at lower-reach sites (Table 3(c), Figure 3(c)) but not the number of euryhaline species (Table 3(d), Figure 3(d)). Because of the low number of lower-reach sites with tilapia ($n=2$), it was difficult to judge their effect on species assemblages. Across all sites, certain fish taxa appeared less sensitive to the effects of *Oreochromis* spp. introduction or reduced forest cover. These fish were largely generalist feeders and included *Ambassis miops*, *Awaous ocellaris*, *Hypseleotris guentheri*, *Sicyopterus lagocephalus*, and *Sicyopus zosterophorum*.

Priority sites for conservation

The 10 mapping units with the highest score for intact connectivity are shown in Figure 5. They include the remote, largely undeveloped regions in Cakadrove and Macuata provinces (Udu Point, Qelewara, Natewa) and Bua province (Kubulau, Wainunu, Dama) of Vanua Levu, as well as the northern and eastern side of Taveuni. Two smaller mapping units of Viti Levu, Naikorokoro and Sawakasa, scored ninth and tenth, respectively, due to the low density of roads and creek crossings and reasonable, proportional amounts of mangroves and reef. The mapping units with the lowest scores (zero or below) were largely situated around the highly agricultural centres of Nadi, Ba, and Labasa, which each have high urban population density, considerable forest clearing for sugar cane, extensive road networks for agriculture and logging, and records of introduced fish species. The Yarawa and combined Kolovisilou–Nubulotulotu catchments on the central Coral Coast of south Viti Levu also had low scores owing to high REP, records of introduced fish and little area or complexity of mangroves and coral reefs.

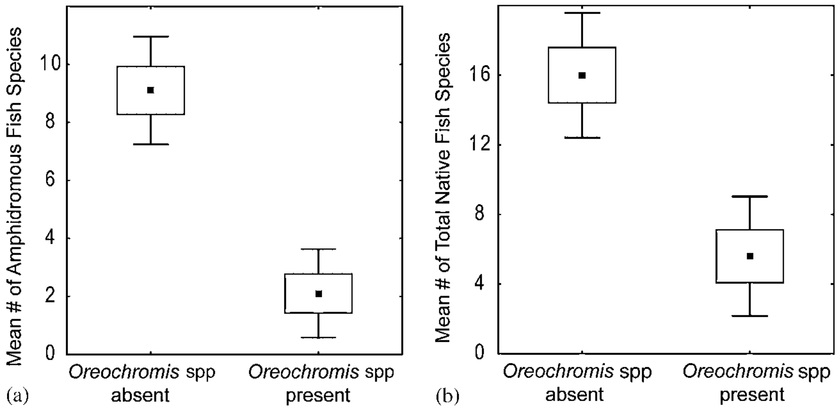

Figure 4. Mean differences in (a) amphidromous fish species number and (b) total native fish species number between mid-reach catchments sites where *Oreochromis* spp. is present and absent. Boxes represent ± 1 standard error and whiskers stretch across 95% confidence interval.

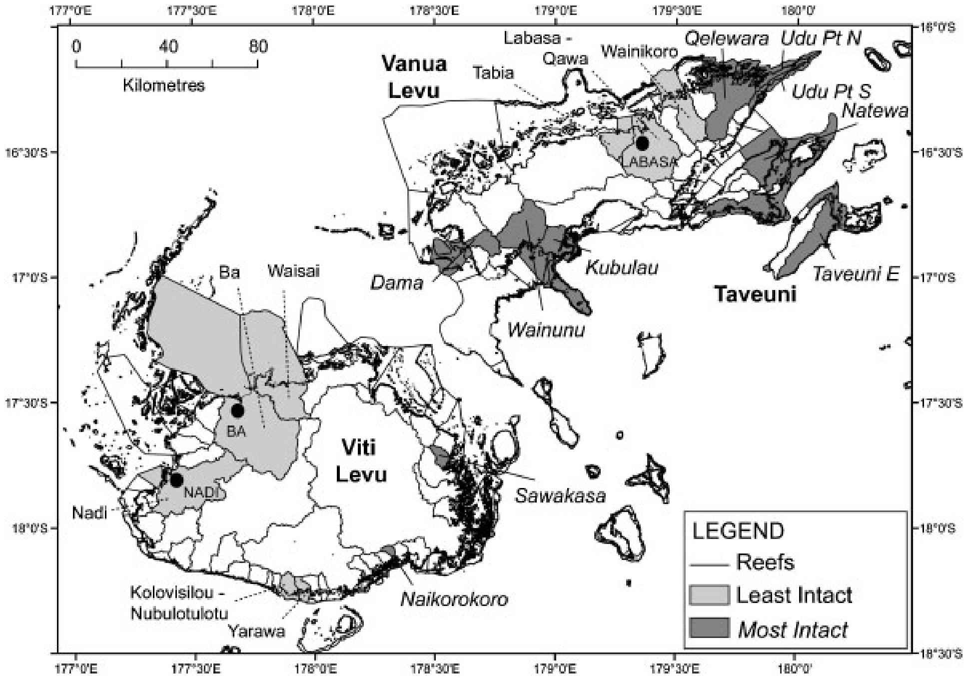

Figure 5. Mapping units (merged catchments with adjacent fishing grounds) that had the most intact (dark grey, solid line) and least intact (light grey, dashed line) connectivity between terrestrial, freshwater, estuarine and marine areas on the main islands of Fiji.

DISCUSSION

Differences in species assemblages between islands and larger land masses

There are two main differences between the freshwater fish composition of large, continental land masses and those of smaller, oceanic high islands in the Pacific: (1) greater numbers of freshwater residents in the former; and (2) higher proportion of diadromy in the latter, particularly through the distinct form of amphidromy. Geologic history probably plays the greatest role in determining present-day characteristics of the species assemblages. The freshwater fish of northern Australia and southern New Guinea are closely related at the generic and familial level, as the land masses have only become recently separated since sea-level rise following the past ice age (~ 10 000 years ago) (Löffler, 1977; Allen, 1991). The land masses of Australia and southern New Guinea are geologically older than most of the oceanic Pacific islands. The long geologic history has allowed considerable freshwater radiation in families mostly considered to be of marine origin (Allen, 1991), including Melanotaenidae, Terapontidae, Clupeidae, Engraulidae and Plotosidae. Because of the large river basin size in northern Australia and southern PNG (relative to small, oceanic islands), there has been greater potential for population isolation and evolution of separate freshwater breeding populations. There is also a distinct lack of primary freshwater fishes in the tropical, western Pacific east of Weber's line (Banarescu, 1990; Allen, 1991), except for those found on continental land masses.

By contrast, most Pacific high islands are geologically young. The current freshwater populations may be at least partially derived from ancestors on islands that no longer exist, owing to the constant formation and disappearance of land at subduction zones and hot spots (Heads, 2006). The temporal impermanence of island waterways has led to species diversification within advantageous life history strategies, such as amphidromy, that allow population persistence through recolonization of newly available freshwater habitats. Given that most volcanic island catchments are small and nutrient-limited, diadromous fish have greater opportunity to seek out favourable habitat for feeding and growth. Of the amphidromous fish, most fall within the families of Gobiidae and Eleotridae (Fitzsimons *et al*., 2002). Gobies of the sub-family Sicydiinae contribute the highest levels of endemism and diversity on tropical Indo-Pacific archipelagos (Keith, 2003), in part facilitated by prodigious climbing ability of many of the species (Blob *et al*., 2007). Amphidromy, however, is not a viable strategy for populations of fish occupying mid to upper reaches of larger river systems (e.g. Sepik-Ramu, Fly) because of the high likelihood of larval starvation before the fish larvae reach the sea (Iguchi and Mizuno, 1999; Keith, 2003).

In many cases, the relatively young age of most Pacific islands (and the Sepik-Ramu system; Coates, 1993) has precluded the development of large estuarine systems equivalent to those in northern Australia or southern New Guinea. As such, estuarine-dependent taxa, such as Centropomidae and Soleidae, are not found in Fiji or other tropical high islands. Other taxa commonly resident in estuaries, such as *Ambassis* spp. and *Glossamia* spp., have diversified extensively within Australia and southern New Guinea. While diversification has led to higher absolute numbers of freshwater fish species and endemics on continental land masses, oceanic islands such as Fiji and Vanuatu have higher species and endemism density when the species richness is adjusted for land area (Abell *et al*., 2008).

Mechanisms for species decline in degraded catchments

The two factors that were most correlated with fish species number in mid-reach catchments of Fiji were the presence of invasive *Oreochromis* spp. and catchment forest cover. Of all fish in mid-reach communities, amphidromous gobiids, which have the highest levels of endemism in oceanic islands of the Indo-Pacific (Keith, 2003; Jenkins *et al*., 2008), were most strongly affected. On its own, loss of natural catchment vegetation cover has been shown to be associated with substantial reductions in native fish and invertebrate biodiversity (Haynes, 1999; Weijters *et al*., 2009). Similarly, declines in native species have been observed after establishment of *Oreochromis* spp. populations (Reinthal and Stiassny, 1991; Lever, 1996). However, the effects of each factor are often coupled, as invasive fish are more likely to establish and have high abundance in degraded streams (Leprieur *et al*., 2008; Linde *et al*., 2008). The following section discusses possible mechanisms by which the combination of degraded land cover and introductions of *Oreochromis* spp. have reduced mid-reach fish diversity, particularly of sensitive amphidromous species, although proof of causation will require independent, experimental verification. As there were only two lower-reach sampling sites with *Oreochromis* spp., it is hard to generalize about their effects on native fish assemblages in these downstream areas, except to say that reduced forest cover is negatively correlated with species numbers.

It is well-documented that intensive logging and large-scale agriculture can increase sediment delivery to catchment waterways and instream turbidity (Davies and Nelson, 1994; Neil *et al*., 2002; Houser *et al*., 2006). Thick, terrestrial sediment settling in pools and riffles can smother habitat and benthic food sources for bottom-dwelling native fish, such as most Fijian gobioids (Gobiidae and Eleotridae). These fish prefer clean rock or rubble substrate as habitat for resting and laying eggs (Keith, 2003). In addition, because many sicydiine gobies are algal scrapers, the availability of benthic algae on which they feed may be reduced (Lord and Keith, 2008), particularly from slash and burn clearing in riparian zones (Iwata *et al*., 2003). For instance, sensitive species such as *Sicyopus* sp., *Stiphodon rutilaureus*, *Stiphodon* sp. 1, and *Akihito* sp. were absent from Fiji rivers with muddy substrate, including the Kilaka and Suetabu, which are *Oreochromis*-free and have relatively intact forest cover.

Increased sediment deposition is equally likely to have consequences on lower trophic levels, and therefore indirect consequences on native invertivore specialists. In a study of Fiji macroinvertebrate fauna in streams from a recently logged catchment compared with those from an undisturbed catchment, Haynes (1999) found consistently lower diversity in the logged area streams over the 3 year study period. She hypothesized that the paucity of neritid gastropods in streams of the logged catchment was due to sediment covering the periphyton on which they grazed (Haynes, 1999). The decline of these prey species may strongly affect fish such as gudgeons that feed preferentially on bottom-dwelling invertebrates. In a study from Tasmania, Davies and Nelson (1994) found an 80% reduction in macroinvertebrate abundance between control sites upstream of logging and downstream sites where riparian buffer width was less than 30 m. In a tropical example, Iwata *et al*. (2003) showed decreases in abundance and diversity of aquatic insects, shrimp, crabs and benthic-dwelling fish with increases in fine sediments, eroded banks and depositional habitat.

In catchment waterways with introduced *Oreochromis* spp., their nesting and foraging behaviour can further impair instream water quality through bioturbation (Starling *et al*., 2002; Canonico *et al*., 2005), and once established, *O. niloticus* may take over all existing habitat (McKaye *et al*., 1995). However, the species absent from mid-reach streams with *Oreochromis* spp. may be differentially affected based on life history, maximum adult body size and feeding guild. *Oreochromis* spp. are known to consume fish larvae and juvenile fish (Froese and Pauly, 2009); the larvae and post-larvae of all sensitive amphidromous species may suffer predation both during downstream and upstream migrations. Smaller-bodied adults, for example *Lentipes kaaea* and *Redigobius bikolanus* (maximum size 4 and 4.2 cm, respectively; Larson 2001; Watson *et al*., 2002) are equally vulnerable. Larger-bodied piscivores, such as *Lutjanus argentimaculatus*, may be indirectly affected by loss of smaller-bodied fish. Visual predators, such as *Belobranchus belobranchus*, *Butis amboinensis*, *Giurus hoedti*, and *Kuhlia rupestris*, may not be able to locate prey items in muddy conditions exacerbated by *Oreochromis* spp. bioturbation.

Several of the sensitive species to disappear in Fiji mid-reach sites with invasives are able to tolerate muddy substrate (e.g. *Butis amboinensis*, *Giurus hoedti*, *Ophiocara porocephala,* and *Redigobius bikolanus*), therefore they may be more affected by predation. Typically, tropical island mid-reach streams do not have many midwater predators (Ryan, 1991). Therefore, introduced omnivores have the potential to strongly affect native fish assemblages. Although introduced poecilliids are known to be tolerant of degraded stream conditions and will eat eggs of other fish (Lever, 1996), they do not appear to have had strong effects on Fiji freshwater fish. This is probably because, as live-bearers, they do not act to lower water quality further through bioturbation.

Fish species that cross the greatest number of habitats (e.g. Groups I and II) are likely to be disproportionately affected by deleterious environmental conditions due to the greater probability of encountering an obstacle to free passage (Eikaas and McIntosh, 2006). Larvae and post-larvae of amphidromous fish are particularly vulnerable during their downstream and upstream migrations. Obstacles preventing their safe passage upstream may be man-made (e.g. dams; Greathouse *et al*., 2006), consequences of non-native fish introductions (e.g. predation by invasives; Canonico *et al*., 2005), and/or consequences of degraded water quality (e.g. reduced ability to feed; Rowe and Dean, 1998). Although species with unique climbing abilities, such as many sicydiine gobies, would be less impeded by physical obstacles, many appear sensitive to degraded water quality conditions. Furthermore, if degraded water conditions are sensed before upstream migration, they may serve as a complete barrier to recolonization. Data from the Scheldt River of Western Europe indicate that the hypoxic zone in the tidal estuary effectively blocked anadromous spawners from returning to their natal spawning sites upstream (Maes *et al*., 2007). If altered water quality conditions can affect chemical cues for migrations of temperate species, it is possible that freshwater pulses from degraded streams may upset cues for tropical, amphidromous juveniles to move into those waterways.

Decline of native fauna from Fiji rivers has had socioeconomic as well as ecological consequences. Village elders recall plentiful harvests of large gudgeons (e.g. *Bunaka gyrinoides* and *Ophiocara porocephala*), which form an important part of the diet of inland communities in Pacific islands (Ryan, 1991). However, the Fiji Department of Fisheries has recently noted a reduction in their market sales (A. Batibasaga, pers. commun), reflecting a decline in wild populations and loss of this important traditional food source. In addition, intact Pacific island systems support up-river migrations of juvenile amphidromous species which form important commercial and cultural fisheries (Ryan, 1991; McDowall, 2007). In Fiji, a kilogram of whitebait (post-larval migrants of sicydiine gobies and possibly some eleotrid species) can sell for up to \$45–\$60 kg^{-1} (Fiji Department of Fisheries, pers. commun.). Where Pacific island hydrologic networks are still intact, arguments by development agencies such as the Food and Agriculture Organization (FAO) for introducing tilapia to improve food security therefore seem unfounded.

Several species appeared to be more resistant to the effects of forest cover loss and invasive species. These fish are generally ubiquitous throughout the Indo-West-Pacific (Froese and Pauly, 2009). The majority of the hardy species (*Awaous ocellaris*, *Hypseleotris guentheri*, *Sicyopterus lagocephalus*, and *Sicyopus zosterophorum*) are amphidromous, and have long larval durations of up to 5 months (Radtke *et al.*, 1988). The long larval duration, broad physiological tolerances and generalist feeding strategies may have resulted in higher relative fitness in degraded habitats.

Some of the other observed patterns in Fiji streams could be explained by small-scale variability in habitats sampled. For example, although both the Suetabu and Kilaka rivers are dominated by muddy bottoms within the lower reaches, the Suetabu also has patches of sand along river bends where the endemic *Glossogobius* sp.1 was found. In addition, although *Belobranchus belobranchus* and *Schismatogobius vitiensis* were not found in catchments with tilapia or low forest cover, both species are cryptic and difficult to sample because of their habit of hiding under rubble and may be present but undetected.

Management recommendations

Terrestrial, freshwater and marine ecosystems have historically been studied and managed separately because they have very different physical conditions, productivities and food webs. Yet, protecting stream habitat alone is not enough to preserve native freshwater fauna on tropical, high islands (Reinthal and Stiassny, 1991; Lord and Keith, 2008); the maintenance of a corridor between forest, river, estuary and sea is needed to preserve species with upstream and downstream migrations. An ecosystem approach to management is required that: (1) incorporates conservation of forests at or above 50% of catchment area; and (2) actively excludes introduction of *Oreochromis* spp. into the hydrologic networks. The regions of Viti Levu, Vanua Levu and Taveuni that scored highest for intactness of aquatic migratory pathways all had high forest cover, in most cases with forest stands that have already been identified as priority sites for conservation in Fiji (D. Olson, unpublished data). Conservation of remaining natural stands will help achieve the goal of the Fiji Department of Forestry to preserve 40% of all extant natural forest (corresponding to 20% of Fiji's original natural forests; Sue, 2007). Preservation of forest cover becomes all the more pressing in the face of global climate change, which may lead to more frequent and extreme disturbance events in the near future (Timmerman *et al.*, 1999) that could exacerbate erosion and sediment transport into catchment waterways. For the lowest scoring regions, forest restoration, particularly around riparian zones, is recommended. Buffer zones are likely to provide additional benefits in terms of stream temperature, protection from bird predation, food availability, and as sources of woody debris (Naiman and Decamps, 1997).

Traditional, community-based management of catchment areas in Fiji has already been successful at preserving native fish diversity in freshwater systems. For example, the small, coastal catchment of Macuata-i-wai, which is surrounded by heavily cultivated and degraded land, had much greater fish diversity than non-managed catchments with comparable forest cover (Figure 3(a), (b)). For 2 years before sampling, the community leaders had strictly enforced a ban on logging, fishing and waste disposal within the vicinity of the stream, which may have preserved the clean, rocky substrate preferred by species such as *Stiphodon* sp. 1, and the overhanging riparian vegetation which provides leaf litter detritus on which *Ophiocara porocephala* feeds. Because much of the land and adjacent marine resources are under traditional tenure (Cooke *et al.*, 2000), there is growing momentum in Fiji to integrate ecosystem-based principles into community-driven natural resource management in order to maintain connectivity between terrestrial, freshwater and marine ecosystems. High quality forest habitat will not only help to maintain strong hydrological connectivity, but will also preserve downstream water quality on adjacent reefs (Jupiter *et al.*, 2008).

Lastly, given that introduced *Oreochromis* spp. have even greater effects on native mid-reach fish faunal diversity than forest cover, it is imperative that government and communities prevent the spread of these invasive fish. This will require well-managed aquaculture facilities to avoid spillover into waterways and setting priorities for invasive-free catchments for conservation. All of these factors need to be considered simultaneously in order to preserve migratory pathways for native aquatic fauna. These ecosystem-scale approaches to conservation are only possible through cross-sectoral engagement at national and local levels to protect all island habitats and their interconnectedness.

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APPENDIX A

Complete species list for freshwater fish found in 28 sampling locations across Fiji. Life history classifications, after Elliot *et al.* (2007), include: freshwater resident (FR); freshwater straggler (FS); estuarine migrant (EM); marine migrant (MM); marine straggler (MW); amphidromy (A); obligate catadromy (COB); and facultative catadromy (FC). Feeding guild classes are: detritivore specialist (DS); detritivore generalist (DG); planktivore specialist (PlS); planktivore generalist (PlG); herbivore specialist (HS); herbivore generalist (HG); invertivore specialist (IS); invertivore generalist (IG); insectivore specialist (InS); insectivore generalist (InG); piscivore specialist (PS); piscivore generalist (PG); carnivore (C); and generalist (G). Status categories are: indigenous (IND); endemic (END); and introduced (INT). Plus marks denote species presence in: any of the mid-reach sites (Mid); mid-reach sites with *Oreochromis* spp. (Mid/O); any of the low reach sites (Low); and low-reach sites with *Oreochromis* spp.

Family	Species	Life History	Feeding Guild	Status	Mid	Mid/O	Low	Low/O
AMBASSIDAE	*Ambassis miops* Gunther. 1872	FS	G	IND	+	+	+	+
ANGUILLIDAE	*Anguilla bicolor bicolor* McClelland, 1844	FC	C	IND	+	+	+	+
	Anguilla marmorata Quoy & Gaimard,	FC	C	IND	+	+	+	
	Anguilla megastoma Kaup, 1856	FC	C	IND	+			
APOGONIDAE	*Apogon amboinensis* Bleeker, 1853	EM	PG	IND			+	
	Apogon lateralis Valenciennes. 1832	EM	PG	IND			+	
	Foa fo Jordan & Seale 1905	EM	C	IND			+	
CARANGIDAE	*Caranx papuensis* Alleyne & Macleay,	MM	PS	IND	+	+	+	+
	Caranx sexfasciatus Quoy & Gaimard,	MM	C	IND	+	+	+	+
	Caranx tille Cuvier 1833	MM	C	IND			+	
CARCHARHINIDAE	*Carcharhinus leucas* (Müller & Henle,	MM	C	IND			+	
CHIROCENTRIDAE	*Chirocentrus dorab* (Forsskål, 1775)	EM	C	IND			+	
CICHLIDAE	*Oreochromis mossambicus* (Peters,	FS	G	INT	+	+	+	+
	Oreochromis niloticus (Linnaeus, 1758)	FS	G	INT	+	+	+	+
CLUPEIDAE	*Sardinella fijiense* (Fowler & Bean, 1923)	MM	PIS	IND			+	
CONGRIDAE	*Uroconger* sp.	EM	IS	IND			+	
DIODONTIDAE	*Diodon liturosus* Shaw, 1804	MS	IS	IND			+	
ELEOTRIDAE	*Belobranchus belobranchus* (Valenciennces, in Cuvier & Valenciennes, 1837)	A	PG	IND		+	+	
	Bostrychus sinensis Lacepède. 1801	A	IG	IND			+	
	Bunaka gyrinoides (Bleeker, 1853)	A	C	IND	+	+	+	+
	Butis amboinensis (Bleeker. 1853)	A	IG	IND	+		+	
	Butis butis (Hamilton, 1822)	A	IG	IND			+	
	Eleotris fusca (Forster, in Bloch and Schneider, 1801)	A	C	IND	+	+	+	+
	Eleotris melanosoma Bleeker, 1852	A	C	IND	+	+	+	+
	Giurus hoedti (Bleeker, 1854)	A	IG	IND	+		+	+
	Giurus margaritacea (Valenciennces, in Cuvier & Valenciennes, 1837)	A	IG	IND	+	+	+	+
	Hypseleotris guentheri (Bleeker, 1875)	FS	InG	IND	+	+	+	+
	Ophiocara porocephala (Valenciennces, in Cuvier & Valenciennes, 1837)	A	DS	IND	+		+	+
	Oxyeleotris marmorata (Bleeker, 1852)	FM	C	IND	+	+	+	+
ENGRAULIDAE	*Stolephorus indicus* (van Hasselt, 1823)	MM	C	IND			+	
	Thryssa baelama (Forsskål, 1775)	MM	DG	IND			+	
GERREIDAE	*Gerres filamentosis* (Lacepède, 1801)	EM	IS	IND			+	
	Gerres longirostris (Lacepède, 1801)	EM	IS	IND			+	
GOBIIDAE	*Acentrogobius caninus* (Valenciennes in Cuvier & Valenciennes, 1837)	A	IS	IND			+	
	Bathygobius fuscus (Rüppell, 1830)	A	IG	IND			+	
	Caragobius urolepis (Bleeker, 1852)	EM	IS	IND			+	
	Cristatogobius aurimaculatus Akihito & Meguro 2000	EM	IS	IND			+	
	Ctenogobiops aurocingulus (Herre, 1935)	EM	IS	IND			+	
	Drombus halei Whitley, 1935	A	IS	IND			+	
	Glossogobius bicirrhosus (Weber, 1894)	A	IS	IND	+	+		
	Glossogobius sp.1	A	IS	END	+		+	
	Psammogobius biocellatus (Valenciennces, in Cuvier & Valenciennes, 1837)	EM	IS	IND	+		+	+
	Yongeichthys nebulosus (Forsskål, 1775)	EM	G	IND			+	
	GOBIONELLINAE							
	Awaous ocellaris (Broussonet, 1782)	A	G	IND	+	+		+
	Oxyurichthys ophthalmonema (Bleeker, 1856–57)	EM	G	IND			+	
	Oxyurichthys tentacularis (Valenciennes, in Cuvier & Valenciennes, 1837)	EM	G	IND			+	
	Pandaka sp.	EM	PG	IND			+	
	Redigobius bikolanus [Herre, 1927)	A	G	IND	+		+	+
	Redigobius leveri (Fowler, 1943)	FR	G	END	+	+	+	
	Redigobius roemeri (Weber, 1911)	FS	G	IND			+	
	Schismatogobius vitiensis Jenkins and Boseto, 2005	A	PG	END	+	+		
	Stenogobius sp.1	A	PG	END	+	+	+	+
	OXUDERCINAE							
	Periophthalmus argentilinaalus Valenciennces, in Cuvier & Valenciennes, 1837	EM	IS	IND			+	
	Periophthalmus kalolo Lesson, 1831	EM	IS	IND			+	+
	SICYDIINAE							
	Lentipes kaaea Watson, Keith and Marquet, 2002	A	IS	IND	+			

Family	Species	Life History	Feeding Guild	Status	Mid	Mid/O	Low	Low/O
	Sicyopterus lagocephalus (Commerson, in Lacepède, 1800)	A	HS	IND	+	+	+	
	*Sicyopus zosterophorum (*Bleeker. 1856-57)	A	IS	IND	+	+		
	Sicyopus (c.f. *Juxtastiphodon)* sp.	A	IS	END	+			
	Stiphodon rutilaureus Watson, 1996	A	HG	IND	+		+	
	Stiphodon sp. 1	A	HG	END	+		+	
	Stiphodon sp. 2	A	HG	END	+	+	+	
	Akihito sp.	A	HG	END	+			
HAEMULIDAE	*Plectorhinchus gibbosus* (Hombron and Jacquinot, 1853)	EM	IG	IND			+	
HEMIRAMPHIDAE	*Hyporhamphus dussumieri* (Valenciennes in Cuvier and	EM	G	IND			+	
	Zenarchopterus dispar (Valenciennes in Cuvier and Valenciennes, 1847)	FM	InS	IND	+		+	+
KUHLIIDAE	*Kuhlia marginata* (Cuvier, in Cuvier and Valenciennes, 1829)	COB	IG	IND	+	+	+	
	Kuhlia munda (De Vis, 1884)	COB	IS	IND	+		+	
	Kuhlia rupestris (Lacepède, 1802)	COB	IS		+	+	+	+
LEIOGNATHIDAE.	*Gazza minuta (*Bloch, 1795)	EM	C	IND			+	
	Leiognathus equulus (Forsskål, 1775)	EM	C	IND			+	
	Leiognathus fasciatus (Lacepède, 1803)	EM	C	IND			+	
	Leiognathus splendens (Cuvier, 1829)	EM	C	IND			+	
LETHRINIDAE	*Lethrinus harak* (Forsskål, 1775)	MS	C	IND			+	
LUTJANIDAE	*Lutjanus argentimaculatus* (Forsskål,	FC	PG	IND	+		+	+
	Lutjanus fulviflamma (Forsskål, 1775)	FC	PG	IND			+	
	Lutjanus fulvus (Forster, in Bloch and Schneider, 1801)	FC	C	IND			+	
	Lutjanus johnii (Block, 1792)	FC	PG	IND			+	
	Lutjanus russelli (Bleeker, 1849)	FC	C	IND			+	
MEGALOPIDAE	*Megalops cyprinoides* (Broussonet, 1782)	FC	PG	IND	+	+	+	
MONODACTYLIDAE	*Monodactylus argenteus* (Linnaeus, 1758)	EM	DG	IND			+	
MORINGUIDAE	*Moringua macrocephalus* (Bleeker, 1863)	MS	PS	IND	+	+		
MUGILIDAE	*Liza macrolepis* (Smith, 1846)	FC	PIG	IND			+	
	Liza melinoptera (Valenciennces, in Cuvier & Valenciennes, 1836)	FC	PIG	IND			+	
	Liza subviridis (Valenciennces, in Cuvier *&* Valenciennes, 1836)	FC	PIG	IND			+	
	Liza vaigiensis (Quoy & Gaimard, 1825)	FC	PIG	IND			+	
	Mugil cephalus Linnaeus, 1758	FC	PIG	IND			+	
MULLIDAE	*Parupeneus indicus* (Shaw, 1303)	MM	IG	IND			+	
	Upeneus sulphureus (Cuvier, in Cuvier & Valenciennes, 1829)	MM	IS	IND			+	
	Upeneus vittatus (Forsskål, 1775)	MM	IS	IND			+	
MURAENESOCIDAE	*Muraenesox cinereus* (Forsskål, 1775)	MM	PG	IND			+	
MURAENIDAE	*Gymnothorax polyuranodon* (Bleeker, 1853)	COB	PG	IND	+	+	+	+
	Uropterygius concolor Rüppell, 1838	EM	PG	IND			+	
OPHICHTHIDAE	*Lamnostoma bicolor* [Kaup, 1856)	EM	IS	IND			+	
	Lamnostoma ksmpeni (Weber *&* de Beaufort, 1916)	EM	IS	IND	+	+	+	
	Pisodonophis cancrivorus (Richardson, 1848)	EM	PG	IND			+	
	Yirrkala gjellerupi (Weber a de Beaufort, 1916)	EM	PG	IND	+			
POECILIIDAE	*Gambusia affinis* (Baird & Girard, 1853)	FS	IG	INT	+	+	+	+
	Xiphophorus hellerii Heckel, 1848*	FS	InG	INT	+	+	+	+
SCATOPHAGIDAE	*Scatophagus argus* (Linnaeus, 1766)	FM	HG	IND			+	
SCORPAENIDAE	*Tetraroge niger* (Cuvier, in Cuvier & Valenciennes, 1829)	A	PS	IND			+	
SIGANIDAE	*Siganus vermiculatus* (Valenciennes, in Cuvier & Valenciennes, 1835)	EM	HS	IND			+	
SPHYRAENIDAE	*Sphyraena obtusata* [Cuvier, in Cuvier & Valenciennes. 1829)	EM	C	IND			+	
SYNGNATHIDAE	*Microphis argulus* (Peters, 1855)	FS	IS	IND			+	
	Microphis brachyurus brachyurus (Bleeker, 1853)	FS	IS	IND	+		+	+
	Microphis brevidorsalis (de Beaufort,	FS	IS	IND			+	
	Microphis leiaspis (Bleeker, 1853)	FS	IS	IND	+	+	+	+
	Microphis retzii (Bleeker, 1856)	FS	IS	IND	+	+	+	+
TERAPONIDAE	*Mesopristes kneri* (Bleeker, 1876)	COB	PG	END			+	+
	Terapon jarbua (Forsskål, 1775)	FC	G	IND			+	+
TETRAODONTIDAE	*Arothron immaculatus* (Bloch *&* Schneider, 1801)	EM	DG	IND			+	
	Arothron reticularis (Bloch & Schneider, 1801)	MS	IS	IND			+	
TOTALS	**104 Species**				**49**	**31**	**102**	**31**