*Impact of anthropogenic disturbances on a diverse riverine fish assemblage in
Fiji predicted by functional traits*

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Abstract

1. Anthropogenic disturbances particularly affect biodiversity in sensitive freshwater ecosystems by causing species loss. Thus, measuring the response of species to multiple disturbances is a key issue for conservation and environmental management.
2. As it is not practical to assess the response of every species in a community, we compared the performance of trait and taxonomic-based groupings of species for their abilities to predict species loss in a threatened freshwater fish assemblage. Specifically, we examined responses of a Fijian freshwater fish assemblage to deforestation, placement of anthropogenic barriers (overhanging culverts) and the presence of introduced cichlids.
3. Species grouped by traits showed more consistent responses to disturbances than taxonomic groups. In particular, species belonging to trait groups that were estuary-associated, favoured medium to hard substrate or feeding specialists were highly likely to be absent in catchments with high deforestation and overhanging culverts. The presence of introduced cichlids (*Oreochromis mossambicus* & *O. niloticus*) had a smaller effect than deforestation and barriers, but was negatively associated with species richness of diadromous species with climbing ability and positively associated with presences of some piscivores. The trait groups also revealed that detritivores, species favouring soft substrate and those with a broad dietary range were less sensitive to anthropogenic disturbances.
4. Our study indicates that using species' traits to predict species loss from disturbed environments can aid in detecting the responses of rare species to disturbance. In addition, we provided a method to estimate the consistency of species' response to disturbance. This study may ultimately help managers identify the most effective actions for conserving sensitive species that are rarely recorded.

Introduction

Biodiversity loss caused by human disturbances is occurring faster than species responses to human disturbances can be measured (Pimm *et al.*, 2014; Rondinini *et al.*, 2014). Species in freshwater ecosystems may be particularly susceptible to local extirpations due to intensive anthropogenic disturbances (Dudgeon *et al.*, 2006). Major threats to freshwater biodiversity include habitat degradation, hydrological modification, water pollution, invasions and overexploitation, with many of the above co-occurring (Schinegger *et al.*, 2012; Stendera *et al.*, 2012). Further, obligate or facultative migrations of many riverine species across connected habitats make them vulnerable to multiple disturbances throughout river networks (Pringle, 2001; Dudgeon *et al.*, 2006). Discriminating the impacts of multiple disturbances is thus a key challenge for designing appropriate conservation interventions to address the threats most likely to cause species loss (Light & Marchetti, 2007; Mouillot *et al.*, 2013).

While it is not practical to assess the response of every species individually, the response of one species to a disturbance can be predicted from the known responses of closely related or functionally similar species. However, rarely has the performance of different methods for assessing species' responses to disturbance been evaluated. Taxonomic ranks are commonly used to group species (e.g., by how species in different families/genera respond to specific disturbance, Weilhoefer (2011)). However, taxonomic ranking methods have several weaknesses, including: biases by errors in taxonomic classification; lack of mechanistic links between species occurrences and environmental characteristics; and inability to compare sites with different species compositions (Mouillot *et al.*, 2006; Verberk, van Noordwijk & Hildrew, 2013). As a result, trait-based analysis has been proposed as an alternative method for assessing the impact of disturbances on species within communities (Reynolds, Webb & Hawkins, 2005; Darling, McClanahan & Côté, 2013; Mouillot *et al.*, 2013).

Biological traits characterize associations between species or functional groups and their environments (Mouillot *et al.*, 2011). Thus, trait-based analysis is a useful tool for predicting how fish communities may respond to human disturbances (Dolédec & Statzner, 2010; Mouillot *et al.*, 2013) or natural gradients (Heino, Schmera & Erős, 2013). Previous studies focused on the relationship between single traits and single environment factors or disturbances but failed to consider how combinations of traits affect species' responses to

disturbances (Verberk, van Noordwijk & Hildrew, 2013). Some recent studies have addressed how combined trait groups respond to a single disturbance (e.g., deforestation in Teresa, Casatti and Cianciaruso (2015)) or how certain traits respond to multiple disturbances (e.g., migration requirement in Branco *et al.* (2012)). Further studies are needed to assess the impacts of multiple disturbances on combinations of traits (Verberk, van Noordwijk & Hildrew, 2013).

Tropical oceanic islands have extraordinarily high levels of endemism due to their geographic isolation and are highly vulnerable to human disturbances (Smith, Covich & Brasher, 2003; Fordham & Brook, 2010; Keppel *et al.*, 2014). Furthermore, because island riverine systems tend to be smaller, less complex and have fewer life history types than continental river systems, disturbance impacts may be more readily apparent (March *et al.*, 2003; Smith, Covich & Brasher, 2003). In this study, we selected tropical oceanic islands in Fiji to assess impacts of multiple disturbances on data-poor native riverine fish communities. Lower abundance and richness of Fijian native fish have been recorded in sites with low forest cover, upstream of overhanging culverts and in the presence of introduced cichlids (Jenkins *et al.*, 2010; Jenkins & Jupiter, 2011; Jupiter *et al.*, 2012). In other locations, the presence of cichlids is associated with degraded habitats (Linde *et al.*, 2008), and cichlids may alter native community composition through competition and/or predation (Canonico *et al.*, 2005; Martin *et al.*, 2010). However, the specific changes to community composition caused by different disturbances remained unclear. The main purposes of this study were to: (1) assess whether fish species grouped by traits or by membership of higher taxonomic groups respond similarly to human disturbances; (2) assess and then predict how human disturbances impact the composition of riverine fish communities; and (3) determine whether taxonomic or trait groups of species loss are better predictors of a species' response to human disturbances.

Methods

Field data were collected by Wetlands International-Oceania and the Wildlife Conservation Society between 2006 and 2012. We assigned freshwater fish species into groups according to (1) life history types (based on Potter *et al.* (2015)); (2) climbing ability; (3) habitat preferences; and (4) feeding guilds shown in Table 1. Then, we assessed relationships between fish groupings and several major disturbances (deforestation, downstream overhanging culverts and the presence of introduced cichlids) shown to affect Fijian

freshwater fish community composition (Jenkins *et al.*, 2010; Jupiter *et al.*, 2012) with statistical models.

Study sites and fish surveys

Riverine surveys were carried in the three largest islands among the Fiji island archipelago (12 - 22°S and 176°E - 178°W), Viti Levu (10,642 km²), Vanua Levu (5,807 km²) and Taveuni (437 km²). Rivers in Viti Levu and Vanua Levu have steep upstream reaches, coastal floodplains and well developed estuaries, but rivers in Taveuni are shorter with fewer estuaries (Jenkins *et al.*, 2010). Data were collected from 107 sites over a range of catchment sizes, river reaches and seasons in order to investigate the impact of disturbances across multiple habitat types (Appendix 1). We also sampled sites with different combinations of disturbances (low to high forest cover combined with presence/absence of downstream overhanging culvert or presence/absence of cichlids). Sites were distributed randomly throughout catchments on three islands and approximately six sites (low, middle and upper reaches in dry and wet season) were sampled per river on seven large river systems in Vanua Levu (Dreketi, Labasa, Qawa, Tabia, Nataqaga, Kilaka, and Suetabu).

Multiple techniques were used to sample riverine fish, including electrofishing with Deka 3000, Marsberg, Germany (600 V, 10A) or Smith-Root, New Zealand (500 V, 10A) backpack unit, netting with gill nets (645.16 mm² mesh), seine nets (40 mm² mesh), pole seine nets (1 mm² mesh) and hand nets (1 mm² mesh), and snorkelling as described in Jenkins *et al.* (2010). Fish were identified to species and assigned into groups based on biological traits (details below) for further analysis. Sampling locations were recorded with a Garmin GPS map 76Cx and water quality variables including temperature, electrical conductivity and dissolved oxygen were also recorded with a handheld YSI multimeter.

Species trait selection and grouping

We selected species traits based on hypothesized links between traits and species' responses to disturbances (Table 1). Trait data were extracted from a published online database (Froese & Pauly, 2015) and previous studies (Ishihara & Tachihara, 2008; Jenkins *et al.*, 2010; Jenkins & Jupiter, 2011; Maie, Schoenfuss & Blob, 2012; Gupta, 2016). We applied Generalized Gower's distance matrix after Pavoine *et al.* (2009) to assess similarities among species, in which feeding guilds, habitat preference and climbing ability were binary variables, and life history was a categorical variable. We coded feeding guild and habitat

preference as multiple binary variables to allow for multiple categories that overlapped across different traits. For instance, piscivores had a 1 for fish and 0 for other food items while carnivores had 1 for fish, invertebrate and insect but 0 for plant and detritus. A functional dendrogram calculated from the distance matrix was used to assign species into trait groups. We selected the level of groups from the dendrogram to create two sets of groups for further analysis and compared the results with grouping by taxonomic ranks. The number of trait groups was chosen to be comparable with the number of taxonomic groups (superorder, order and suborder).

Statistical analysis

The ordinal relationship between the species' trait dissimilarity matrix and the community compositional matrix (species presence/absence in survey sites) was visualized using a double principal coordinate analysis (DPCoA) (Pavoine, Dufour & Chessel, 2004). DPCoA is similar to principal coordinate analysis (PCoA), but it can plot both species (trait group) and community (site) similarity data on one multidimensional space (i.e., double PCoA), and the ordination of sites accounts for similarities in species' traits. Thus, plots of the ordination indicate the position of sites with respect to species similarity across species traits. We used DPCoA plots to visualize the similarities among species trait groups (derived from the functional dendrogram described above), so that plots of the response of species richness to disturbances were on axes represented the similarity of trait groups. Then we separated survey sites into low-reach and mid/upper-reach sites (e.g., Jenkins and Jupiter (2011)) to account for the effect of natural factors such as salinity and stream width on the following analysis. Both salinity and stream width are significantly higher ($p < 0.05$) in low-reach sites than mid- and upper-reach sites, but no significant difference was found between mid- and upper-reach sites by pairwise t-test.

We used binomial generalized linear models (GLMs) to estimate how the proportion of species richness from each group varied across disturbance gradients. The binomial distribution is a model for proportions when observing a known number of binary trials (Zuur *et al.*, 2009). In this case we observed for each trait/taxonomic group the number of species occurring at a site out of the maximum number of species belonging to that group. Thus, the response variable was binomial, in that we modelled the number of species observed at a site out of the total number of species in each group. Species in each group were modelled as

$$\text{logit}(P_{ij}) = \alpha + \beta_1 \times \text{ForestCover}_i + \beta_2 \times \text{OverhangingCulvert}_i + \beta_3 \times \text{Cichlids}_i$$

, in which P_{ij} is the proportional species richness in site i for trait/taxonomic group j and β is the regression parameter for each disturbance. Explanatory variables included the percentage of forest cover in catchment (continuous variable between 0 and 100), the presence of downstream overhanging culverts (binary variable) and the presence of cichlids (binary variable). A quasi-binomial model was used when over-dispersion was detected (Zuur *et al.*, 2009). We also conducted t-tests to assess the independency between disturbances such as the forest cover in sites with versus without overhanging culvert or with versus without introduced cichlid. Because no overhanging culverts were observed at any low-reach site, explanatory variables for low-reach sites only included forest cover and the presence of cichlids.

We used the GLMs to predict expected proportional species richness for each group across the disturbance gradients and calculated area under receiver operating characteristic curve (AUC) to assess model fit. Jackknife resampling was applied on groups to evaluate the consistency of responses within every group by removing species from each group one at a time and then calculating the AUC for that species using the remaining species in the trait group to build the model. This approach tests the assumption that species within a given group are similar enough that rate of species loss can predict presence/absence of a single species. If there was only one species in the group, AUC was applied without Jackknife resampling by evaluating the model fit of that species to itself. Taxonomic groups by suborder, order and superorder were also analysed for comparison with trait groups. All analyses were conducted in R (R Core Team, 2015) with the packages “MASS” (Venables & Ripley, 2002), “ade4” (Dray & Dufour, 2007), and “cvAUC” (LeDell, Petersen & van der Laan, 2015).

The expected changes in community structure predicted by the GLM were visualized by plotting predicted species richness (proportional species richness multiplied by the total species richness in a group) of every group for low and high disturbance levels (Mouillot *et al.*, 2013). We made plots to present the impacts from each disturbance on predicted species richness, which included 90% and 10% forest cover, presence or absence of overhanging culverts and presence or absence of cichlids. We also plotted the percentage change in species richness after disturbance to compare the impacts of each disturbance across groups.

Results

A total 123 native and 4 introduced fish (cichlids (*Oreochromis mossambicus* & *O. niloticus*), mosquitofish (*Gambusia affinis*) and swordtail (*Xiphophorus hellerii*)) species from 36 families and 11 orders were recorded from 18 low-reach and 89 mid/upper-reach sites (Appendix 2). Sixty-two species were only recorded in low-reach sites and seventeen species were only recorded in mid/upper-reach sites. Three species, the dusky sleeper (*Eleotris fusca*), giant mottled eel (*Anguilla marmorata*) and rainbow gudgeon (*Hypseleotris guentheri*), were found at around half of all survey sites. Thirty-one species were only recorded at one site and only 2 (Perciformes and Anguilliformes) out of 11 orders were found in more than one third of sites. Among all native species sampled, 58 species were recognized as diadromous, 59 as estuarine-associated and 6 as freshwater species.

Trait groups and observed communities

We used the dendrogram of species' trait similarities to characterize two separate groupings (Fig. 1: #1 and #2). The #1 partition on the dendrogram separated species into four groups by life history types and climbing ability (A: diadromous without climbing ability; B: estuary-associated without climbing ability; C: freshwater without climbing ability; D: diadromous with climbing ability) and #2 further separated species into 12 groups by habitat preference and feeding guild. The number of species within groups varied from 1 (G: diadromous, without climbing ability and detritivore & H: diadromous, without climbing ability, piscivore and medium substrate) to 53 (B: estuary-associated and without climbing ability).

Most estuary-associated species (53 out of total 59 species in this group) and diadromous species with no climbing ability (40 out of 43) were recorded in low-reach sites while there were fewer estuary-associated species (14 out of 59) and diadromous species with no climbing ability (26 out of 43) in mid/upper-reaches (Fig. 1). On the contrary, only half (8 out of 15) of total diadromous species with climbing ability were found in low-reach sites but all 15 species were present in mid/upper-reach sites. Almost all freshwater species could be found in both low- and mid/upper-reach sites.

Estuary-associated species with no climbing ability were found in sites with more than 50% forest cover and no downstream overhanging culverts and a greater proportion of freshwater species were observed in sites with medium to high forest cover. Some diadromous species and the species with climbing ability were more prevalent across sites with a variety of

disturbances. No obvious pattern was found between groups and the presence of cichlids.

Trait groups and predicted communities

We focused on survey sites in mid/upper-reaches in flowing sections as most species groups in lower reaches, using both trait and taxonomic grouping methods, had no significant relationship with the disturbances measured in this study (Appendix 3: tables 1 & 3).

Fig. 2 shows the predicted species richness in each trait group predicted by GLMs with and without specific disturbance. The species richness of estuary-associated species and fishes without climbing ability declined significantly (or near significantly) at sites with lower forest cover (Fig. 2: a & d) and upstream from overhanging culverts (Fig. 2: b & e). More than half of the groups showed significant positive relationships with forest cover and the presence of an overhanging culvert. Less than a quarter of groups had significant or near significant ($0.05 < p < 0.1$) relationships with the presence of cichlids (GLM results in Fig. 2 & Table 2). Low forest cover (10%) was associated with lower species richness throughout trait groups when compared to high forest cover (90%). Overhanging culverts had variable impacts on trait groups (Fig. 3). The predicted number of estuary-associated species was ~70% lower in streams with overhanging culverts when compared to streams without culverts. Further, the number of diadromous species without climbing ability and the number of freshwater species was ~45% lower in streams with overhanging culverts. Interestingly, the presence of an overhanging culvert was also associated with a lower (~55% lower) number of species with climbing ability. Therefore, we conducted further analysis to estimate the relationship between the presence of overhanging culverts and the proportion of species with climbing ability among all species (included species without climbing ability) by GLMs. The proportion of species with climbing ability in habitat with at least one overhanging culvert was predicted to be higher than in habitat with no overhanging culverts (regression coefficient: 0.571 and p : 0.041). The presence of cichlids had a wide range of effects (from 35 - 190%) on predicted species richness, but only four groups showed significant or near significant relationships. No significant difference in forest cover was found in sites with, versus without, the presence of overhanging culverts ($p = 0.394$) or sites with, versus without, cichlids ($p = 0.100$), respectively.

Comparison of trait and taxonomic groups

Fewer significant relationships with human disturbances were observed when grouping species by taxon than by traits (Table 3). Forest cover and overhanging culverts had more

significant or near significant relationships with species richness than the presence of cichlids (Appendix 3: Table 2). Forest cover had significant or near significant relationships for one superorder group (Acanthopterygii), two order groups (Perciformes & Syngnathiformes), and five suborder groups (Gobioidei, Percoidei, Syngnathoidei, Muraenoidei & Anguilloidei); overhanging culverts with two superorder groups (Acanthopterygii & Elopomorpha), two order groups (Perciformes, & Anguilliformes), and four suborder groups (Gobioidei, Percoidei, Muraenoidei, & Anguilloidei); and presence of cichlids with no superorder and order groups, but one suborder groups (Gobioidei).

Mean AUC values above 0.65 and standard errors mostly < 0.05 indicated moderately consistent responses of species to disturbances within both trait and taxonomic groups (Tables 2 & 3). AUC values support our hypothesis that species loss within a group is a proxy for presence/absence of individual species. The AUC values of species differed only slightly between grouping methods (taxonomic versus trait) and the level of group aggregation (Table 3). Lower AUC values (< 0.6) were found in a few trait groups such as F (diadromous, without climbing ability, planktivore, preferring soft substrate), J (estuary-associated, without climbing ability, invertivore), N (freshwater, without climbing ability, carnivore or generalist, preferring medium substrate) and O (diadromous, with climbing ability, mainly carnivore, preferring medium to soft substrate) (Table 2). The species that had low AUC values were similar regardless of grouping methods. Species with low AUC values included eels (*Anguilla* spp.), rarely recorded species (*Mugilogobius notospilus* & *Glossogobius* sp. 2) and *Awaous* gobies.

Discussion

Our results suggested that deforestation, overhanging culverts and introduced cichlid may change the abundance and richness of Fijian native fish, finding that are comparable to previous studies (Jenkins *et al.*, 2010; Jenkins & Jupiter, 2011; Jupiter *et al.*, 2012). In addition, trait-based and taxonomic grouping approaches allow greater insight into how riverine fish respond to multiple disturbances. We found that deforestation and overhanging culverts are associated with the greatest declines in richness of Fijian riverine fish communities, suggesting management actions should find ways to ameliorate these threats. Both trait and taxonomic groups showed a reasonable ability to predict the responses of most individual species to disturbances, having similar AUC values. However, trait based groupings were more sensitive detectors of environmental responses in that they were more

likely to detect significant relationships between species loss and disturbance. Further, trait grouping is suggestive of the ecological processes that cause species loss in disturbed environments.

The ability to link biotic traits to disturbances makes trait groups more sensitive to environmental change and their response is more consistent across spatial and temporal scales than for taxonomic groups (Culp *et al.*, 2011). However, in a disturbed system, the response of individual species within one functional group can be profound and cause failure in models that assume species within groups respond to disturbance more similarly than species in different groups (Fong & Fong, 2014). We applied a novel Jackknife resampling to evaluate the consistency of response within groups by using the other species within the same group to predict the presence/absence of one species. The results indicated the consistency within most groups and that the rate of species loss could be a reasonable surrogate for individual species presence/absence. However, the AUC values reported here are much lower than those for freshwater fish in other regions and indicate further work is required to accurately predict the response of the Fijian fish fauna to disturbances (Bond *et al.*, 2011). For instance, we found that the occurrence rates of species with flexible habitat use (e.g., *Anguilla* spp., Arai, Chino and Le (2013)) and species that were rarely recorded in the field surveys (e.g., *Mugilogobius notospilus*, & *Glossogobius* sp. 2) were poorly predicted by other species within the same trait or taxonomic group.

Comparing predictive ability of traits versus taxonomic groups

The use of traits to categorize species allowed us to combine survey sites with various species compositions (around 42% of species only recorded in one or two sites) and provided more direct linkages between fish community change and specific disturbances. Although species within the same taxonomic group might share similar life history traits and so respond to disturbance similarly (i.e., high AUC values for taxonomic groups that have a significant relationship with disturbance), taxonomic groupings may be inappropriate in some cases (e.g., particularly in highly diversified groups). Communities such as those in oceanic islands that are dominated by a few diverse taxa might mask the responses of functionally different species within a specific taxonomic group (i.e., fewer significant relationships with disturbance). For instance, one of the mostly widely distributed and diversified taxonomic groups, Gobioidae, was significantly impacted by all disturbances. However, these significant relationships were the combination of various responses between

different traits (almost every trait group has at least one species from Gobioidae) and disturbances spread across many genera and species. Furthermore, the number of species was distributed more evenly among trait groups than taxonomic groups. As most prevalent species belong to only a few taxonomic groups (e.g., Perciformes, Gobioidae and Poeyidae) and many taxa only occurred in a few sites or with lower species numbers, the taxonomic groups may be more likely to be biased by a few data points.

In Fiji, several riverine fish have been recorded as new species or new records recently and some species have relatively confined distributions (e.g., Jenkins and Mailautoka (2010); Larson (2010); Copeland, Boseto and Jenkins (2016)). In addition, strong seasonal variations of species composition have been found in Fijian rivers (Jenkins & Jupiter, 2011). Species' traits might be more suitable in this case for their stability through spatial and temporal scales and sensitivity to disturbances (Culp *et al.*, 2011).

Impacts from anthropogenic disturbances and the implications for management

The broad impact of deforestation across different life history types and mobility can threaten biodiversity and ecosystem function in Fijian rivers. Particularly, deforestation may impact on specialist feeding guilds and species that prefer medium to hard substrate. Species that have specific diet or habitat requirements may be more vulnerable to habitat degradation (Teresa, Casatti & Cianciaruso, 2015) while generalists may be less affected because they can take advantage of various habitats (Devictor, Julliard & Jiguet, 2008). In this study, nearly all trait groups contained endemic species that were predicted to be impacted by deforestation (e.g., *Redigobius leverii*, *Schismatogobius vitiensis*, and *Mesopristes kneri*). While the responses of species to disturbances within most groups were consistent, trait-based analysis can provide a precautionary warning for rare or cryptic species that are difficult to sample such as *Belobranchius belobranchius* and *S. vitiensis* (Jenkins *et al.*, 2010). Studies in Fiji suggest that maintaining at least 50% of catchment forest cover can retain most riverine fish species (Jenkins *et al.*, 2010; Jupiter *et al.*, 2012). Furthermore, forest protection can benefit downstream coral reef condition by prevention of terrestrial runoff and sedimentation (Klein *et al.*, 2014). Thus, a comprehensive forest protection plan is critical to secure river, terrestrial and marine biodiversity and ecosystem function.

Overhanging culverts mainly impacted on migratory species and species that lacked climbing ability. The impact of barriers on riverine species might affect species presence more significantly than pollution or habitat modification in tropical islands because

diadromy is the most prevalent life history type (Hein *et al.*, 2011; Ramírez *et al.*, 2012). In Fiji, over 98% of fish in rivers use saltwater habitats during their life cycle (Jenkins *et al.*, 2010). In addition to diadromous species, our results further reveal estuary-associated fishes can also be impacted by barriers. As many marine or estuarine species use riverine habitats for feeding, breeding or to escape predation (Jenkins & Jupiter, 2011; Potter *et al.*, 2015), barriers might impact both upstream and downstream fish communities by blocking migration routes and reducing available habitats for estuary-associated species. Interestingly, while barriers can also impact the species with climbing ability, the proportion of species with climbing ability among all species increased in the habitat upstream of barriers. Indeed, barriers might benefit species which can climb by hindering predators without climbing ability (e.g., estuary-associated species) while meanwhile increasing the predation pressure on other species that live downstream of barriers (Cooney & Kwak, 2013). Because many diadromous (e.g., gudgeon, flagtail, goby and eel) and estuary-associated fish (e.g., snappers, jack, trevally and barracuda) are socioeconomically important species for inland and coastal fisheries in Fiji (Jansen, Parkinson & Robertson, 1990; Jenkins *et al.*, 2010), improving the connectivity of existing culverts for native species can help restore river ecosystems and benefit local fisheries.

The role of exotic species as a primary driver for native species declines, or as a passive interloper taking advantage of highly modified habitats, varies by ecological situation (e.g., MacDougall and Turkington (2005) vs. Hermoso *et al.* (2010)). As no significant correlation between disturbances was observed, the changes in fish community composition with the presence of cichlids might suggest impact from cichlids (or other disturbances that have not been examined in this study) instead of deforestation or overhanging culverts. Some native piscivores showed positive associations with the presence of cichlids indicating possible similarities in preference of habitat. Nevertheless, the lack of patterns between cichlids and certain traits could indicate the influence of other factors such as the locations of aquaculture activities (where introduced cichlids were reared) or species traits that have not been included in this study, such as small body size enhancing potential vulnerability to predation by cichlids. Previous studies in Fiji have found the absence of many small-bodied amphidromous fish in catchments where cichlids were recorded (Jenkins *et al.*, 2010).

While studies on the impact of introduced cichlids on tropical island ecosystems are limited, caution must to be taken with cichlid introductions because of their potential impact on native species (Jenkins *et al.*, 2010; Russell, Thuesen & Thomson, 2012). Nevertheless,

since the 1940s, cichlids have been introduced to many Fijian rivers and have become an important protein source for locals in rural and inland areas (Costa-Pierce, 2002). In addition, high tolerance to stressors and flexible life history traits give them the advantage to thrive in degraded habitats (Russell, Thuesen & Thomson, 2012), thus they should remain a core component of freshwater aquaculture initiatives where they are already established. Further studies about the distribution of cichlids and how they interact with native species and overall protein availability are recommended for environmental impact assessment.

Future work and conclusions

Lack of comprehensive trait data for some endemic or rare species and flexible traits (e.g., facultative migration or local adaptation) among some populations might affect the power of trait-based analysis (Culp *et al.*, 2011). Therefore, studies on the biological traits of native fauna and local populations can improve the power of a trait-based predictive approach. In addition, incorporating other traits that might link to specific disturbance (e.g., body size as discussed above or hypoxia tolerance) can reveal further relationships between species and disturbance. Applying Jackknife resampling when calculating the ability of trait groups to predict species response can also help to evaluate the consistency within groups.

In conclusion, this study developed a trait-based analysis that revealed impacts from various disturbances on Fijian riverine fish communities and provided information for guiding environment management. Deforestation can cause significant impacts on fishes across life history and mobility types, while overhanging culverts primarily hinder the movement of species without climbing ability. The presence of cichlids had less impact in comparison but can reduce the richness of diadromous species with climbing ability (a group that contains the most endemic species) while being associated with the presence of some piscivores. The results indicate that trait-based analysis can help to identify the impacts from deforestation, overhanging culverts and the presence of introduced cichlids on riverine fish communities and predict the community responses.

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Table 1. Disturbances and relevant traits used in this study. Trait categories are derived from classifications in Elliott *et al.* (2007) and data are extracted from FishBase (Froese & Pauly, 2015) and previous studies (Jenkins *et al.*, 2010; Maie, Schoenfuss & Blob, 2012; Jenkins & Jupiter, 2011; Ishihara & Tachihara, 2008; Gupta, 2016).

Disturbance	Deforestation	Overhanging culvert	Presence of cichlids
Possible impacts	Increased fine sedimentation may smother resting or feeding habitat and affect hunting ability of visual predators(Jenkins <i>et al.</i> , 2010). Increased nutrient loads that may drive metabolic activity and decrease dissolved oxygen concentrations (Weijters <i>et al.</i> , 2009).	Connectivity loss that hinders movement of migrants (Makrakis <i>et al.</i> , 2012).	Bioturbation of bottom sediment, predation on small-bodied individuals, competition for resources. Possible indicator for other disturbance(s) (e.g., low dissolved oxygen) (Russell, Thuesen & Thomson, 2012).
Relevant traits	Habitat preference and feeding guild (Teresa, Casatti & Cianciaruso, 2015)	Life history type and climbing ability	All traits
Trait categories	<i>Habitat preference</i> : generalist or substrate preference from soft (mud), to hard (rock) <i>Feeding guild</i> : detritivore generalist/specialist, planktivore generalist/specialist, herbivore generalist/specialist, invertivore generalist/specialist, insectivore generalist/specialist, piscivore generalist/specialist, carnivore and generalist	<i>Life history type</i> : freshwater, diadromous or estuary-associated <i>Climbing ability</i> : yes or no	All categories

Table 2. Regression coefficients and p values from GLMs between trait groups and disturbances in mid/upper-reach sites. P value: *** < 0.001; ** < 0.01; * < 0.05; + < 0.1. AUC represent the means and standard errors (SE) of the AUC as calculated across all species within that group using Jackknife resampling. There are no standard errors for groups G and H because those groups only had one species. All species in group L were recorded in low-reach sites only and the results are in Appendix 3: Table 1.

Groups	Forest cover	<i>p</i>	Culver t	<i>p</i>	Cichlids	<i>p</i>	AUC (SE)
# 1							
A	0.018	**	-0.860	***	-0.276		0.664 (0.042)
B	0.023	+	-1.174	*	0.518		0.688 (0.038)
C	0.019	**	-0.613	*	-0.081		0.607 (0.079)
D	0.008	+	-0.983	***	-0.542	*	0.712 (0.052)
# 2							
E	0.017	**	-0.844	***	-0.266		0.653 (0.047)
F	0.016		-0.428		-16.633		0.318 (0.091)
G	0.034		-0.722		-17.200		0.786
H	0.224	*	-18.775		3.494	+	0.718
I	0.029		-1.581	+	-0.824		0.721 (0.126)
J	0.048		-0.031		1.041		0.535 (0.126)
K	0.010		-1.583	*	1.122	+	0.759 (0.073)
L	-		-		-		
M	0.018	*	-0.797	*	-0.005		0.626 (0.041)
N	0.025	*	-0.465		-0.198		0.353 (0.074)
O	-0.002		-0.702	**	-0.485	+	0.580 (0.046)
P	0.027	**	-1.439	***	-0.548		0.823 (0.044)

Table 3. Number of significant ($p < 0.05$) and near significant ($0.05 < p < 0.1$: within parentheses) relationships between trait or taxonomic groups and disturbances. AUC represent the means and standard errors (SE) of the area under the ROC curve when species were removed from a group one at a time.

Grouping (number of groups)	Forest cover	Culvert	Cichlids	AUC (SE)
Trait group				
# 1 (4)	2 (2)	4	1	0.676 (0.025)
# 2 (11)	5	5 (1)	(3)	0.645 (0.027)
Taxonomic group				
Superorder (2)	1	2	0	0.677 (0.025)
Order (6)	2	2	0	0.670 (0.027)
Suborder (11)	3 (2)	3 (1)	(1)	0.667 (0.027)

Figure legends

Fig. 1. Dendrogram (from Generalized Gower's distance matrix) of the trait similarities of 125 species. The partitions #1 and #2 show where the two levels of classification were derived. Species richness represents the number of species in each group for low-reach (L) and mid/upper-reach (MU) sites.

Fig. 2. Predicted species richness with (red) and without (blue) disturbances from two sets of trait groups, partition #1 (a - c) and #2 (d - f) on the dendrogram of trait similarities. Letters A to P represent trait groups from Fig. 1. Positions of each trait group were determined with DPCoA, such that closer trait groups are functionally more similar than distant trait groups. The size of dot represents species richness and “*” and “+” means significant ($p < 0.05$) and near significant ($p < 0.1$) relationship, respectively. (a) & (d): 90% (blue) and 10% (red) forest cover; (b) & (e): without (blue) and with (red) downstream overhanging culvert; (c) & (f): without (blue) and with (red) cichlids.

Fig. 3. Percentage change in species richness from low to high disturbance levels (defined in Methods) for trait groups with significant and near significant relationships. The upper and lower hinges of the box correspond to the first and third quartiles. The upper and lower whiskers represent the range within $1.5 * \text{IQR}$ (inter-quartile range) of the upper and lower hinge, respectively.