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Merging connectivity rules and large-scale condition assessment improves conservation adequacy in river systems

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Summary

1. Conservation adequacy is defined as the ability of conservation measures to sustain biodiversity. In riverine ecosystems, this has until recently been inhibited by not considering the high level of connectedness in planning frameworks. While connectedness is important for maintaining key ecological processes and ensuring persistence of biodiversity, it also facilitates the propagation of threats along river networks, which may compromise the conservation of freshwater biodiversity. This paper aims to introduce two modifications to river conservation planning related to connectivity and catchment condition that together improve the adequacy of the priority areas identified. This will establish an operational framework for end users, such as policy makers and NGOs.
2. We operationalise the connectivity framework that has recently emerged in systematic conservation planning for rivers by using a GIS coding system for catchment management in the conservation software package Marxan. Additionally, we use a landscape measure of catchment disturbance to direct the conservation plan to the least disturbed area while still meeting targets for the conservation of fish species as surrogates for overall biodiversity in our study catchment, the Daly River in northern Australia. This disturbance measure aggregated information on land-use, extractive industries, point-source pollution, and water infrastructure.
3. We successfully modeled the distribution of 39 fish species based on GIS derived landscape descriptors (discharge, distance to river mouth, geology and conductivity being most important).

4. Results from the systematic planning analysis identified a portfolio of watersheds that delivered close to optimal upstream protection with around 4700 stream kilometres (30% of the total network). When using upstream disturbance as an extra penalty, most of the network stayed intact, however a replacement area was found for a major tributary - only adding an extra 1% to the total area.

Synthesis and applications: Improving adequacy by accounting for upstream connectivity and condition in an easily useable framework - as well as a software package - has the potential to facilitate further application of systematic methods in river conservation planning. Furthermore, integrating condition as a discounting factor can also improve adequacy in terrestrial or marine environments, while not necessarily leading to more costly solutions.

Introduction

In the last two decades, systematic conservation planning has emerged as a burgeoning research enterprise for spatial allocation of resources for conservation management. The central goal of systematic conservation planning is the representation of biodiversity in conservation area networks, ensuring its persistence into the future, and achieving these goals with as much efficiency as possible (Margules & Sarkar 2007). Systematic conservation planning has until recently been primarily concerned with terrestrial and marine environments (e.g. Ball, Possingham & Watts 2009; Pressey *et al.* 2009) and has received limited attention in freshwater ecosystems. This was due, in part, to the challenge of deploying available methodologies to riverine systems that are characterized by dendritic or distributory channel networks that drain upstream catchments and connect critical habitats along longitudinal dimensions (Abell, Allan & Lehner 2007).

Greater incorporation of longitudinal connectivity has been achieved recently (Linke, Norris & Pressey 2008; Moilanen, Leathwick & Elith 2008; Roux *et al.* 2008; Linke, Turak & Nel 2011). For example, Hermoso *et al.* (2011b) modified the MARXAN algorithm (Ball, Possingham & Watts 2009) – one of the most widely employed conservation planning packages - to include a flexible penalty for not including upstream catchments in a conservation plan, thus explicitly linking conservation value of riverine environments with connectedness to other upstream parts of the riverine network . In addition to incorporating connectivity in conservation planning, the condition or integrity of those connected areas also needs to be considered. Various means of quantifying condition exist based on site-specific assessments of biota such as macroinvertebrates (e.g. Simpson & Norris 2000; Clarke, Wright & Furse 2003), fish (eg. Kennard *et al.* 2005; Kennard *et al.* 2006; Hermoso *et al.* 2010) or habitat conditions (Parsons, Thoms & Norris 2004). The application of GIS and remote sensing has enabled condition assessment to be extended to broader spatial scales (Stein, Stein & Nix 2002; Norris *et al.* 2007) and facilitated the incorporation of condition into conservation planning.

To date indicators of condition have only been directly included in a handful of studies to prioritise areas for biodiversity conservation. Linke and Norris (2003) described a two-stage process: if condition had significantly declined, the site was deemed 'not worthy' of a conservation assessment, only sites in good condition were included in a conservation prioritisation. However, conservation features, such as rare species, may occur only in degraded landscapes, in which case they are poorly considered in the planning process. To overcome this potential problem in a conservation assessment undertaken in Victoria (Australia), Linke *et al.* (2007) prioritised all sub-catchments and taxa simultaneously and then prescribed actions based on condition and vulnerability. Sub-catchments in good condition that were highly vulnerable to future threats were flagged as priorities for protection, while degraded areas of high conservation value were earmarked for restoration. Similar approaches – in which condition was either used as a pre-processing step to filter out degraded areas or a post-hoc analysis have been carried out in North America, South America and South Africa in recent years (Thieme *et al.* 2007; Khoury, Higgins & Weitzell 2011; Nel *et al.* 2011).

However, post-hoc comparisons lack in efficiency as they often prescribe unrealistic scenarios. If condition is not included in the actual prioritisation, highly degraded areas can be picked over areas in better condition. Removing degraded areas after running a planning algorithm, undermines the efficiency of systematic conservation planning. In 2011, studies in Belize (Esselman & Allan 2011),and the Yangtze

(Heiner *et al.* 2011) integrated condition into a single framework for conservation planning by including an environmental risk surfaces as a penalty in a MARXAN analysis. For this, they summed all upstream disturbances and treated them as a cost in the optimisation algorithm.

The aim of this paper is to formally integrate upstream condition into a general connectivity framework by merging upstream connectivity rules (Hermoso *et al.* 2011b) and condition discounting (Esselman & Allan 2011; Heiner *et al.* 2011) with a large-scale condition assessment (derived from Stein, Stein & Nix 2002). In the Daly River (tropical northern Australia), we draft a conservation plan based on modelled distributions for 39 freshwater fish species, while considering upstream protection using a connectivity algorithm (Beger *et al.* 2010). Instead of an *a posteriori* contrast of actions (Linke *et al.* 2007), we then include a large-scale condition assessment as a penalty function which will act in a similar way to the risk surfaces used by Esselman and Allan (2011). In contrast to Esselman and Allan (2011) however, the additional connectivity penalty will design more compact priority areas for conservation.

Methods

Study area

The Daly River catchment (Figure 1) encompasses 53 000 km^2 and is vegetated primarily by tropical savannah woodland. The river and its catchment are in relatively good environmental condition compared to other major rivers in Australia. Annual rainfall in the catchment averages 1000 mm, with 90% falling during the wet season months between November and May. Rainfall is negligible during the dry season, with flow in the Daly River and its major tributaries supplied predominately from groundwater inputs from underlying karstic aquifers. Perennial flow distinguishes the Daly River from most other rivers of the wet/dry tropics of northern Australia, which cease to flow for a large proportion of the dry season. (Kennard *et al.* 2010). The Daly catchment has important ecological, cultural and economic values (Jackson *et al.* 2008; Chan *et al.* in press). The dominant land-uses are low density cattle grazing and conservation areas (including a few major national parks), although small parts of the catchment have been cleared for more intensive land-uses such as urbanization, pasture and agriculture. The Daly River is currently unregulated, with only a small volume of groundwater extracted annually for agriculture, but there is considerable pressure for further agricultural development and water demand, particularly in the vicinity of Katherine and the Douglas–Daly region (Figure1, Stewart-Koster *et al.* 2011; Chan *et al.* in press)

Fish sampling

Fish surveys were conducted at 55 locations throughout the Daly River catchment during the dry seasons of 2006 and 2007 (Fig. 1). High river flows and access constraints due ti widespread flooding precluded wet season fish sampling. Sampling sites were selected according to a stratified random sampling design (i.e. randomly stratified by river size) to encompass as much of the natural biological and environmental variation as possible, but was constrained by available access points to the river. Within each sampling site (500–1000m reach length), fish were collected at multiple discrete locations within each site using a boat-mounted, generator-powered electrofishing unit (Engineering Technical Services Model MBS-2DHP-SRC with pulsed DC current) or a backpack-mounted, battery-powered electrofisher (SmithRoot Model 12B). These samples are hereafter termed electrofishing ‘shots’ with each shot fixed to five minutes duration (elapsed time). Water conductivities varied widely among study sites (50–600 μs cm−1) so electrofisher output settings were adjusted to maximize efficiency at each site but with the minimum power required to stun fishes (pulsed DC current, <250 pulses s−1, <500 V, <25% duty cycle, maximum 35 A). At least 15 electrofishing 'shots' were usually undertaken at each site, with the intent of sampling the full range of habitats present. At the completion of each electrofishing shot, fish were identified to species level and returned alive to the approximate point of capture. The intensive sampling effort undertaken at each site yields an accurate estimate of species' presence and absence at each study site. In a separate study to be published elsewhere, we evaluated the sampling effort required (i.e. number of electrofishing shots) required to gain accurate and precise estimates of reach-scale species composition (Kennard *unpublished data*) Our analyses show that when compared to data obtained from more extensive sampling using up to 25 electrofishing shots, estimates of species composition from 15 electrofishing shots were highly accurate (95% similar to estimates from more extensive sampling) and precise (coefficient of variation = 0.05). We conclude that our sampling regime provided quantitative estimates of fish species composition and that this data was suitable for species distribution modelling and conservation planning analyses.

Species distribution modelling

Five estuarine vagrant species occurring at one site only were not included in the species distribution model. The remaining 39 species occurred at two or more of the 55 sites and their presence/absence were modelled as a function of a set of environmental predictor variables (see below) using multi-response artificial neural networks (Olden 2003; Olden, Joy & Death 2006) to generate predicted distributions throughout the catchment for each species. Neural networks offer a powerful approach to species distribution modelling due to their ability to model multiple response variables and their higher predictive power (based on empirical and simulated data) compared to traditional and other machine learning approaches (Olden & Jackson 2002). These models associate the occurrence of particular species with environmental attributes at the sites sampled and are used to infer the composition of freshwater fish communities from environmental data in unsampled planning units. Importantly, we did not extrapolate beyond the scope of the model in that we restricted our predictions of species distributions to river segments that were within the range of environmental variation of the 55 model calibration sites. Ten ecologically-relevant landscape-scale environmental variables were selected from a larger number of candidate variables for use in the predictive models of fish species distributions (Appendix 1) which were derived from the National Environmental Stream Attributes database for rivers (see Geoscience Australia 2011 for details). Principal Component Analysis and Spearman's correlations among variables were used to identify and remove highly correlated variables. Absolute Spearman's correlation coefficients among the final set of predictor variables were < 0.5. Environmental predictor variables described hydrology (mean and coefficient of variation in annual discharge, estimated using a catchment water balance model), air temperature (mean annual temperature), river basin topography (distance to river mouth, slope, valley confinement - indicative of the depositional environment and the potential for stream aquifer connectivity) and catchment storage (relative proportion of depositional/floodplain areas in the catchment), substrate hydrogeological properties which can shape ecologically important properties of the stream hydrograph (sedimentary rocks and soil hydraulic conductivity) and vegetation (natural tree cover).

We used feed-forward neural networks trained by the backpropagation algorithm to model spatial variation in species' presence or absence. The architecture of the network consisted of a single input, hidden and output layer. The input layer contained one neuron for each of the environmental variables. The number of neurons in the single hidden layer was chosen to minimize the trade-off between network bias and variance by comparing the performances of different cross-validated networks. The output layer contained multiple neurons; one neuron for each response variable being modelled, representing the probability of species' presence-absence. Model training involved the cross-entropy error function, and learning rate (η) and momentum (α) parameters (varying as a function of network error) were included during network training to ensure a high probability of global network convergence. The contributions of the environmental variables in the neural networks were quantified by calculating the product of the input-hidden and hidden-output connection weights between each input neuron and output neuron and then summing the products across all hidden neurons. This approach is deemed the most appropriate as it has been shown to outperform other techniques for quantifying variable contributions in neural networks (Olden, Joy & Death 2004). All neural network analyses were conducted using computer macros written in the MatLab® (The MathWorks, Natick, Massachusetts, USA) programming language.

Model performance was assessed using n-fold cross validation and summarized using three metrics: overall classification success (percentage of sites where the model correctly predicts species' presence-absence); sensitivity (percentage of the sites where species' presence was correctly predicted); and specificity (percentage of the sites where species' absence was correctly predicted). Our objective was to derive unbiased estimates of species' prevalence by minimising false presences and absences so we used a threshold (i.e., probability threshold above which each species is predicted to occur) in which the predicted prevalence equalled the observed prevalence (as recommended by Freeman & Moisen 2008). We evaluated model performance using the area under the receiver operating characteristic curve (AUC, see Fielding & Bell 1997) based on the n-fold cross validated model predictions. An AUC>0.6 is usually defined as acceptable model performance (Fielding & Bell 1997).

Conservation planning

Identification of priority areas was carried out using the conservation planning software Marxan (Ball, Possingham & Watts 2009). Marxan uses a randomisation procedure called 'simulated annealing' to mimimize costs while maximising conservation features. A third term in the simulating annealing equation is often boundary length, which had been designed in terrestrial settings to produce compact conservation areas: if boundaries are left 'open' a penalty is incurred and the spatial design is less attractive for the optimisation algorithm

$$Objective\ function = \sum_{planning\ units} Cost + SPF \sum_{features} Feature\ Penalty + CSM \sum Connectivity\ Penalty$$

(Equation 1)

where

SPF = a scaling factor for the importance of species penalties

CSM = connectivity strength modifier

In this paper, we used the modification by Hermoso *et al.* (2011b) for riverine settings: instead of penalising for open boundaries, we penalise for unprotected sub-catchments upstream of a selected planning unit, weighted by distance (see Fig 2). The relative importance of this connectivity penalty can be scaled by the parameter CSM (connectivity strength modifier, see equation 1). If CSM is set to 0, the term drops out of equation 1 and a standard conservation planning exercise – without any explicit spatial clumping component – is carried out. In contrast, if CSM is set to a high value, most of the catchment upstream of the selected features needs to be included to minimize the objective function. This effectively creates a 'whole-of-catchment' protection scheme, similar to the heuristic used by Linke *et al.* (2007). As described by Beger *et al.* (2010), we used the asymmetric connectivity function in Marxan. By including this rule, the operators of the conservation planning software can specify whether they want only upstream connectivity, only downstream connectivity or bi-directional connections. In the latter case, different weights can be specified for upstream and downstream connections. In our study, for simplicity and to demonstrate the functionality of the connectivity penalty, we only used upstream connections.

We explored different weights to the connectivity penalty (different CSM values), as well as a penalty for the selection of sub-catchments that are in degraded ecological condition that offer less potential from a conservation perspective. We used the River Disturbance Index (RDI) (Stein, Stein & Nix 2002) – a direct measure of human pressure on rivers - as an indirect measure of ecological condition. RDI values reflect both the spatial extent and potential magnitude of impact on riverine ecosystems of human disturbance. Recently updated index values were derived using geographic data on the extent and intensity of human activities including land-use, urbanization, extractive industries and other point sources of pollution, and water infrastructure. As we are treating RDI as our cost surrogate, we did not include a 'real' monetary conservation cost in the analysis, as in the study by Esselman and Allan (2011). Including a third 'cost' in addition to connectivity and condition would make exploration of the tradeoffs between connectivity and condition harder.

Spatial framework and analysis

We used a nested catchment framework that is a precursor to the Australian Hydrological Geofabric (AHGF, Bureau of Meteorology 2010) as our spatial framework for the conservation planning exercise. Modelled species distributions were mapped to Level 8 stream catchments containing on average 2.77 stream kilometres. In total, a river network length of 15859 km was spread over 5722 sub-catchments. We used the modified version of the Pfafstetter coding scheme (Verdin & Verdin 1999) in the AHGF to describe the spatial dependencies in the catchment. The Pfafstetter coding system describes the network topology of any river network (Fig 2). In any terminal catchment, a river system is split into the four major contributing catchments, as well as connecting sub-catchments. The main stem segments are then coded with uneven numbers between 1 and 9. The four major tributaries are coded with even numbers between 2 and 8. The resulting nine sub-catchments are then again sub-divided in the same way and the digits added to parent sub-catchments (for sub-catchment 2, the resulting sub-divisions would be named 21, 22…29). As demonstrated in Fig. 2, this can be then used to construct a connectivity penalty file for Marxan. Hereby – as discussed in Beger *et al.* (2010) and Hermoso *et al.* (2011b) – the reciprocal distance between two subcatchments is used as the penalty if both subcatchments are not protected. For example, if the distance between two subcatchments is 10 km, the penalty will be 1/10=0.1. At 20 km the penalty is 1/20=0.05 and further diminishing with distance. Using a recursive algorithm, starting from the top sub-catchments, we constructed a connectivity file with a total of 774274 connections between the sub-catchments.

To determine the optimal spatial configuration, we ran Marxan with different CSM values (0, 0.5, 1, 2 and 3) to establish a baseline in which only the area of a sub-catchment is used as a cost. With the optimal CSM determined by plotting a tradeoff curve between the upstream protection and the total area needed, we then added the condition measure RDI as an additional penalty to determine whether optimal spatial allocation of conservation action will change when considering disturbance.

To deal with highly uneven distribution ranges of the fish species, we avoided setting proportional targets that would overrepresent common species and used a fixed number of habitat kilometres instead. As a conservation target, we set 90 stream kilometres for each species. This was chosen after running a sensitivity analysis on different target levels (30 km, 60km, 90km, 120km), which revealed that about 16% of the area was needed when targets were set at 90km. Target setting in this study should however not inform real-life planning scenarios in which practicioners should set targets based on study specific parameters such as species requirements or available conservation resources.

Targets were treated as probabilities, similar to Hermoso *et al.* (2011b): The contribution of a sub-catchment to the targets is calculated as

$$c_{\text{sub-catchment}} = \text{streamlength}_{\text{sub-catchment}} \times \text{probability of occurrence}_{\text{sub-catchment}}$$

(Equation 2)

Thus for example, if a sub-catchment contains 10 kilometres of stream and the probability of occurrence is 1, this then counts as 10 habitat kilometres whereas if the probability of occurrence is 75%, it would count as 7.5 habitat kilometres.

Results

Quantitative sampling of the fish fauna from the Daly River resulted in the collection of 22,214 individuals from 39 species at the 55 study sites. Species frequency of occurrence ranged from 0.02 to 0.98 (mean = 0.32) across the study sites (Appendix

2). The multi-response neural network predictive models exhibited high success in predicting individual species' presence or absence. The correct classification of species presence-absence was generally high (mean = 0.81) and all but five species had correct classification rates exceeding 0.7 (Table 2). Overall, the model was better able to correctly predict the absence of species than their presence (mean specificity = 0.77 and mean sensitivity = 0.54); an expected result given the low frequency of occurrence of many species in the dataset. The model had difficulty predicting the presence of rare species (i.e. low sensitivity) and the absence of some widespread species (low specificity). Nevertheless, generally high AUC values (mean = 0.75) indicate very good overall predictive performance (Table 2). Mean annual discharge and distance to the river mouth were the two most important environmental predictors of species occurrences in the Daly River reference sites (mean relative contribution = 23% and 12%, respectively, Appendix 1). The remaining eight predictor variables individually contributed less than 10% to overall model predictions.

Species distributions ranged from headwater species such as the exquisite rainbowfish (*Melanotaenia exquisite*, Fig 3a), lowland species such as pennyfish (*Danaruisa bandata*, Fig 3b) to diadromous species such as mullet (*Liza ordensis*, Fig 3c) and near ubiquitous species such as black bream (*Hephaestus fuliginosus*, Fig 3d).

When running Marxan with a conservation target of 90 habitat km/species, the configuration without connectivity (Fig 4a, CSM=0) was fragmented, however only 2572 kilometres of the stream network of the catchment were identified as a conservation priority, which corresponds to 16% of the catchment (15859 km in total). By increasing the CSM, a more contiguous upstream reserve network emerged. However, this has the drawback that more of the catchment is flagged in the conservation plan, so 4770 stream kilometres are needed at CSM 1 - increasing to

6562 km at CSM 2 and 8857 km at CSM 3 (Fig 4b-d). Trading off total area needed versus unprotected upstream area *sensu* Hermoso *et al.* (2011), we decided to use CSM=1 for further analysis.

The River Disturbance Index (RDI) suggests that much of the Daly river catchment is in good condition (Fig 5c). The key areas that are under pressure from human activities are the mouth (north-west corner), the western part of the main stem, as well as the Douglas Daly region, just east of the mouth (see Fig 5b). As shown in Fig 5a (indicated by the arrow) this part of the catchment is of very high conservation value and appears in every solution of the conservation plan. To detract from the disturbed catchment, we included the river disturbance index as an additional penalty in Marxan. An almost equally good solution was found by representing the species in the disturbed part of the Douglas Daly in a more southern arm of the catchment that shared the environmental characteristics of the disturbed site (Fig 5c). Only marginally more river kilometres were needed: 4810 km when considering condition versus 4770 km in the initial analysis. Apart from a few upland segments, this swap from the Douglas southward was the main change in conservation area configuration when including condition as a detractor (Fig 5d).

Discussion

This study successfully merges techniques in species modelling and modern systematic conservation planning, thus bringing systematic conservation planning in riverine landscapes closer to a framework that can be applied by end users. We demonstrated how disturbance and therefore condition could be included directly in conservation planning, as opposed to trading off multiple metrics of conservation value, vulnerability and condition (Linke & Norris 2003; Linke *et al.* 2007).

Our multi-response artificial neural network model provided accurate predictions of the distribution of 39 freshwater fish species in the Daly River catchment based on a small set of ecologically relevant landscape scale environmental variables. We found that a conservation plan to represent all 39 fish species in the Daly River consistently identified three key conservation priority areas, irrespective of the choice of connectivity penalty or condition discounting: the upper Katherine River catchment, the main stem of the Daly River channel and the lower Daly floodplain and tributaries. While preliminary, this information provides the first step in the development of a comprehensive and efficient freshwater conservation plan for the Daly River catchment. This could be further refined and improved by the inclusion of other biodiversity surrogate information (e.g. representation of other freshwater-dependent species and/or ecological processes) and socioeconomic costs of on-the-ground conservation actions (e.g. riparian vegetation restoration, feral animal control), and engagement of stakeholders during the planning process.

This study demonstrates how connectivity can be operationalised within a widely used conservation planning package, readily available for end users. The asymmetric connectivity framework in Marxan (Beger *et al.* 2010), combined with an easily constructed connectivity file (Hermoso *et al.* 2011b) has the potential to promote more widespread use of river conservation planning.. Marxan and other freely available conservation planning software packages have helped to mainstream conservation planning. Marxan, for example, is currently used by 700 organisations, including 90 government agencies, all major NGOs, the UN and the IUCN. The Australian Hydrological Geofabric (Bureau of Meteorology 2010) can be used to readily construct both the planning unit framework, as well as the connectivity between planning units. The HydroSHEDS global hydrological framework (Lehner *et* *al.* 2008) delineates spatial units analogous to those in the AHGF. If a smart coding system that allows routing (Pfafstetter or similar) were to be included in HydroSHEDS in the future it would greatly facilitate uptake of modern conservation planning methods in freshwater systems.

As discussed previously, condition assessment has been a mainstay in river management for a century (Norris & Thoms 1999). In past terrestrial and marine studies, current condition has played a smaller role, especially in conservation planning. Most of the direct discounting in conservation planning algorithms has been carried out on future threats – mainly described as vulnerability. Since Margules and Pressey (2000) traded off irreplaceability in their highly influential paper, vulnerability has been used in all realms, terrestrial, marine and freshwater (Wilson *et al.* 2005; Linke *et al.* 2007; Stelzenmuller *et al.* 2010). When condition is added, the framework gets more complicated. For example, Linke *et al.* (2007) added a third axis to the irreplaceability-vulnerability framework and prescribed the nature of the action based on the condition axis: conservation for catchments in good condition, restoration for degraded areas. This however led to two sets of explicit priorities that could not be compared.

It is generally preferred to derive a single set of priorities, instead of producing the multiple conservation/restoration list of Linke *et al.* (2007). This study integrates condition assessment directly into the priority setting by discounting for condition in the prioritisation step. By integrating the two, the priorities are measured in one currency and can be directly compared. Also, the integration removes inefficiencies by duplication; the principle of complementarity (Kirkpatrick 1983; Pressey 2002) dictates that target-based conservation planning algorithms achieve efficiency by avoiding the duplication of desired conservation features. However, if two different assessments – one for restoration, one for conservation– are made, complementarity cannot be considered and efficiency will suffer. Figure 5 demonstrates that the algorithm including a discount for condition does not change most of the priorities – yet it finds a highly efficient solution to replace the degraded Douglas-Daly catchment with only minimally larger effort (1% increase in land area). This ensures the key feature of systematic conservation planning – minimizing impact on stakeholders while maximising conservation outcomes.

Although the framework presented here represents a methodological advancement– especially with respect to ease of implementation and potential broad applicability with landuse and disturbance maps available for many areas worldwide – this application it is still a coarse simplification of the real world. If direct taxa responses to disturbances are available – or up-to-date distributions of conservation features are known, a condition discount might not be necessary. In this case, condition is already included in the distribution models – an approach demonstrated by Hermoso *et al.* (2011a) who contrasted hypothetical and real distribution models in river conservation planning. Of course, this kind of approach will need more detailed ecological knowledge or more refined models and can only apply for species data. If using surrogates or ecoregional targets, a discounting approach can circumvent the need for adjusting ecoregions or surrogates that have changed under human influence.

Including connectivity will have flow-on effects on the persistence of species downstream and the complicated response curves arising from this cannot be included in Marxan. In a conceptual paper, Hermoso *et al.* (2012) describe how the principles of complementarity could be applied in environmental planning when multiple types of management actions (riparian revegetation, catchment reforestation) are used. Instead of just assigning planning units to zones, direct responses of features to disturbances and restoration actions are quantified. This is a further step towards the ‘holy grail’ of mixed-use conservation planning in which generalised species responses could be optimised under multiple actions that include real costings, as well as socioeconomic considerations. While riverine adaptations of proper mixed protection schemes are still under development however, the method described in this paper can be implemented straight away, with both the optimisation tools and most spatial data layers readily available. Furthermore, integrating condition will enhance adequacy of conservation plans and on-the-ground conservation success, not only in aquatic settings but potentially even in a terrestrial environment.

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Figure 1. The study catchment, indicating key tributaries, as well as the 55 sampling sites.

Figure 2. Using a Pfafstetter coded network to construct a Marxan connectivity file. a) An example of the codes on the main stem – even numbers describe tributaries, uneven numbers describe connecting segments of the main stem, b) tributaries are split again and a digit is added to the code , c) this is then translated in a Marxan connectivity file by calculating distances between segments. Close unconnected upstream segments incur high penalties – this penalty diminishes with the reciprocal distance to the downstream segment.

Figure 3. Designing a protected area network for species with different habitat requirements: modeled distributions of a) exquisite rainbowfish (*Melanotaenia exquisite* , ROC AUC=0.96) ,b) pennyfish (*Danaruisa bandata*, ROC AUC=0.99), c) mullet (*Liza ordensis* , ROC AUC=0.95), d) black bream (*Hephaestus fuliginosus* , ROC AUC=0.67)

Figure 4. Change in irreplaceability (expressed as selection frequency after 100 runs) under increasing connectivity requirements. Connectivity is expressed by the Marxan connectivity strength modifier (CSM)

Figure 5. a) Selection frequency at connectivity strength modifier (CSM) = 1 b) river disturbance index in the Daly catchment (red=high disturbance, yellow=medium disturbance, green=low or no disturbance) c) irreplaceability when disturbance is considered in the optimisation d) difference in selected irreplaceability with and without disturbance. Circles in a) and c) indicate area where highest change in irreplaceability occurs when considering condition.

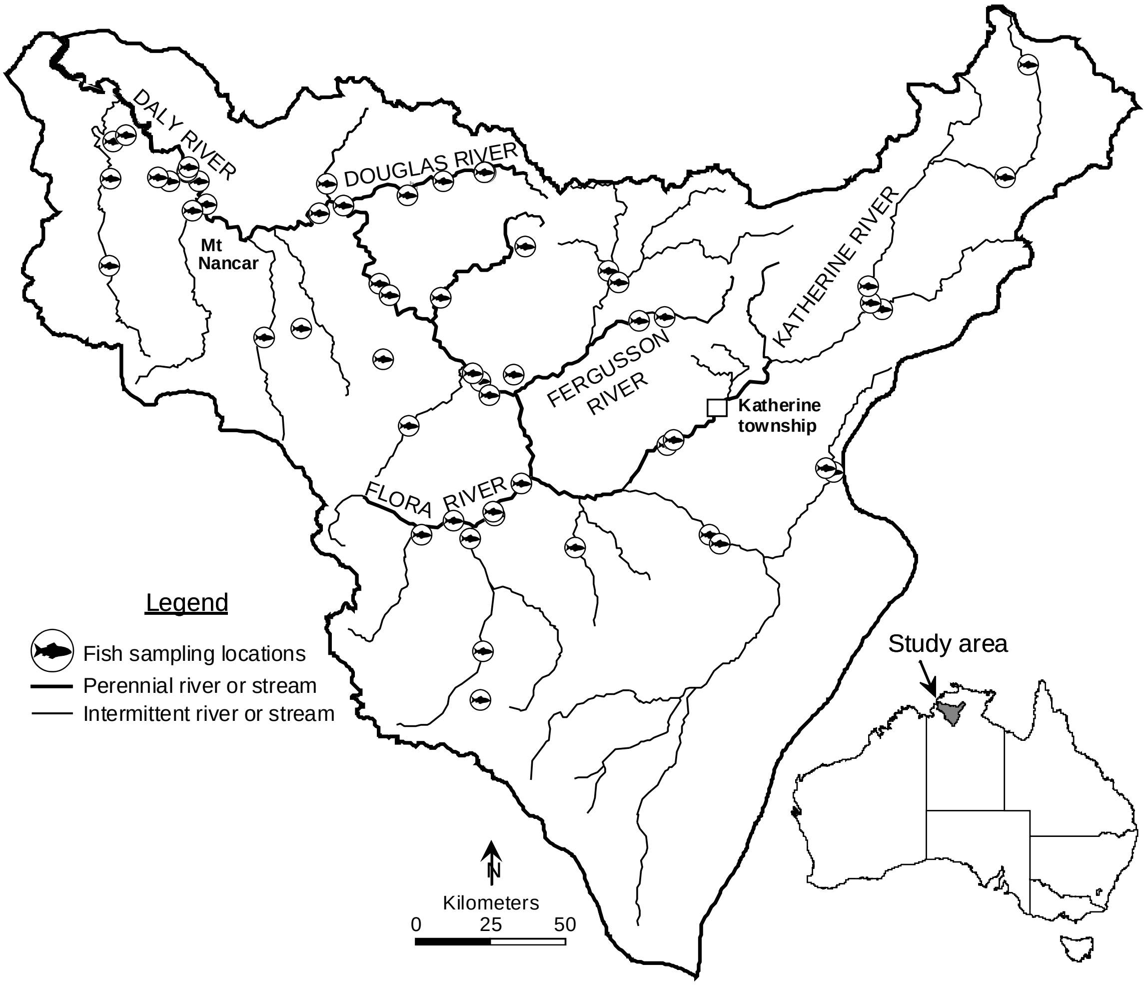

DALY RIVER
DOUGLAS RIVER
Mt
Nancar
KATHERINE RIVER
FERGUSSON
RIVER
Katherine
township
FLORA RIVER
Legend
Fish sampling locations
Perennial river or stream
Intermittent river or stream
Study area
N
Kilometers
0
25
50

Figure 1.

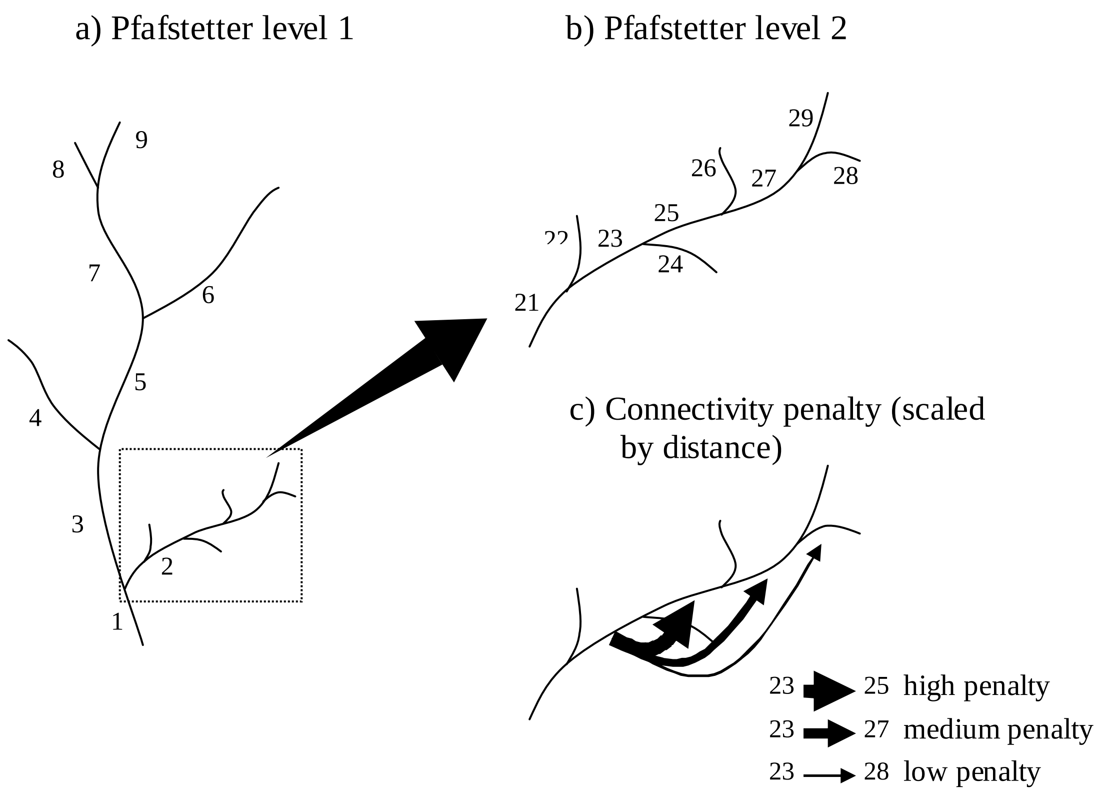

a) Pfafstetter level 1
9
8
7
6
5
4
3
2
1
b) Pfafstetter level 2
29
26
27
28
25
22
23
24
21
c) Connectivity penalty (scaled by distance)
23 25 high penalty
23 27 medium penalty
23 28 low penalty

Figure 2

a b c d

Figure 3

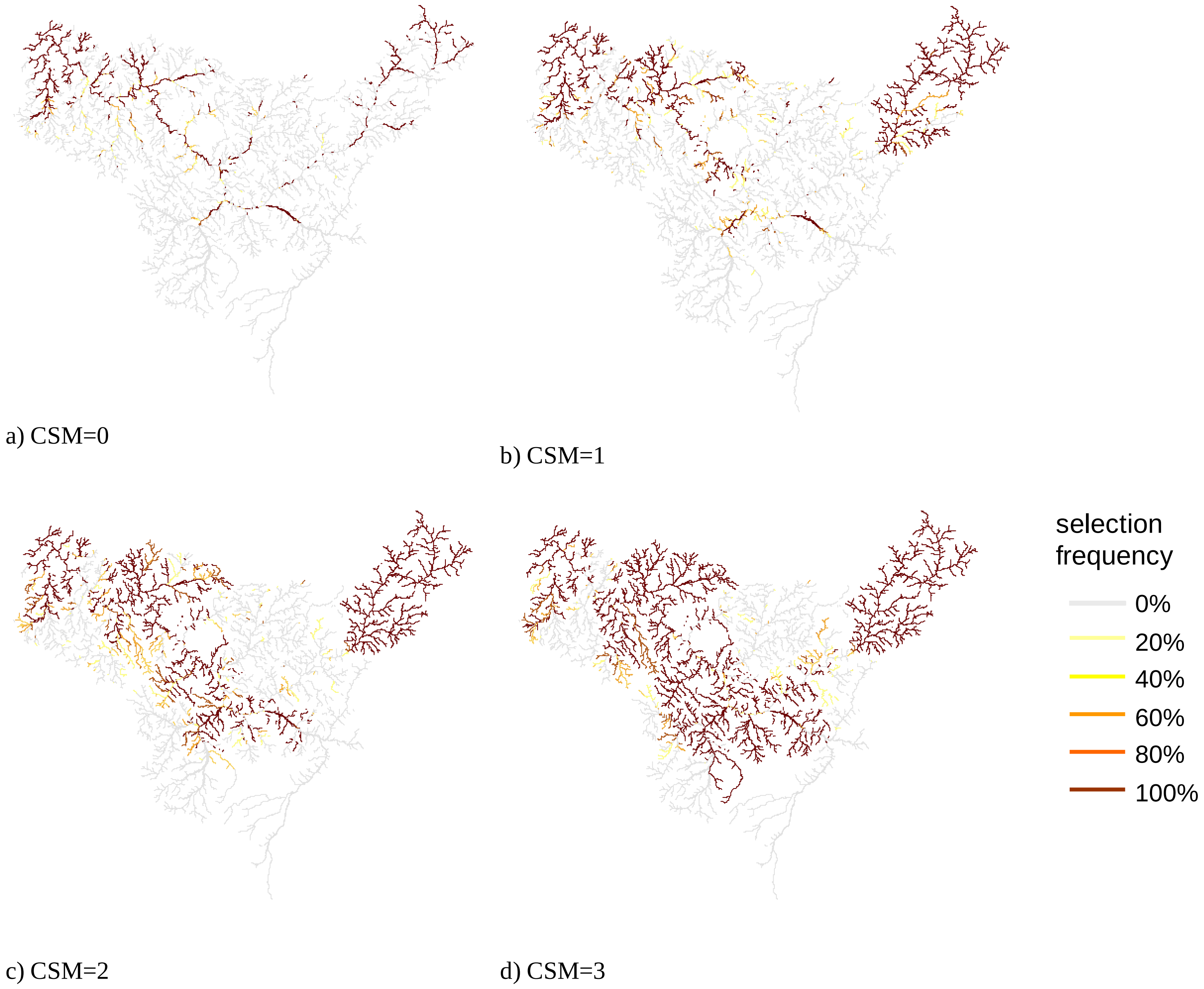
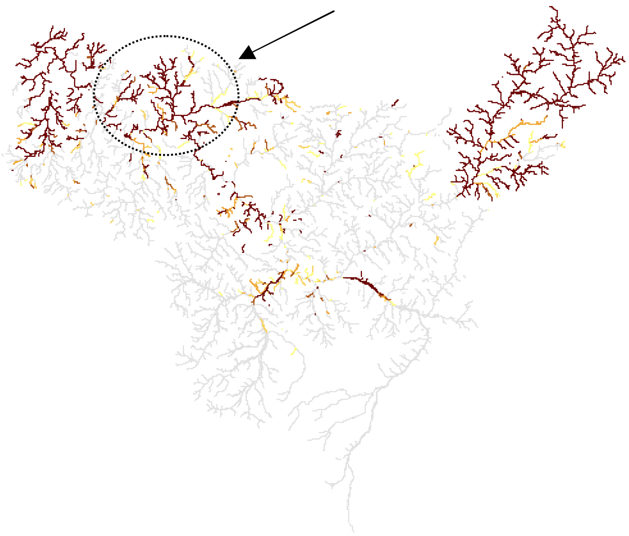
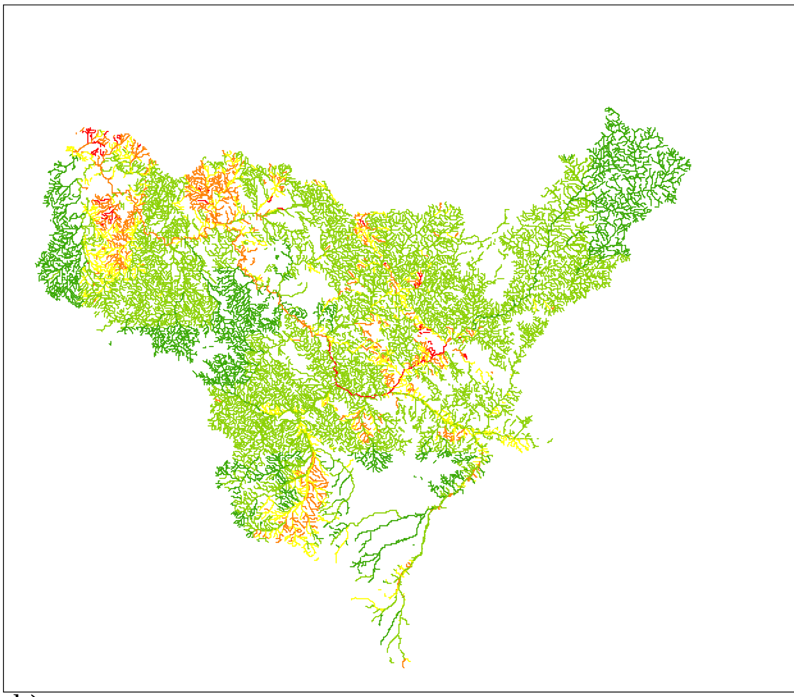

a) CSM=0
b) CSM=1
c) CSM=2
d) CSM=3
selection frequency
0%
20%
40%
60%
80%
100%

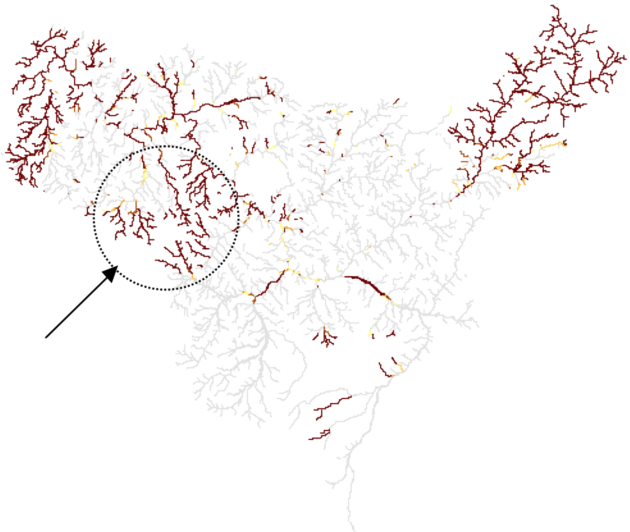
Figure 4



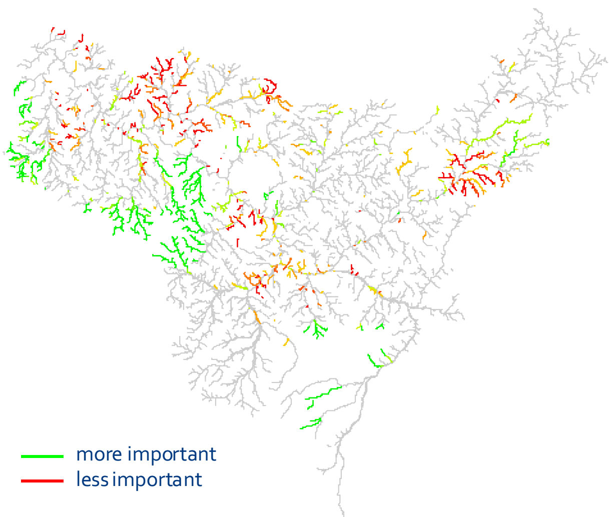
a) CSM=1



b)



c)



d)

Figure 5

Appendix 1 . Range and median values of environmental predictor variables and their mean absolute relative contributions (%) for predicting fish species' presence-absence (averaged across the 39 fish species). For detailed information about the predictor variables see Geoscience Australia (2011)

Variable	**Description**	**Minimum**	**Median**	**Maximum**	**Relative contribution**
Mean annual discharge	Mean annual discharge (GL/year x 10^3)	0.6	229.5	9306.7	21.3
CV annual discharge	Variation (expressed as CV) in annual discharge	0.58	0.79	1.41	8.3
Sedimentary rocks	Catchment siliclastic / undifferentiated sedimentary rocks (%)	0.0	35.3	89.8	9.4
Hydraulic conductivity	Catchment average saturated hydraulic conductivity (mm/h)	30	205	300	6.1
Tree cover	Catchment tree cover (%)	7	72	100	5.7
Temperature	Stream and environs mean minimum annual temperature (oC)	11.4	12.7	14.1	9.6
Valley confinement	Stream reach grid cells and their immediate neighbours that are not valley bottoms (%)	0	21	100	9.7
Slope	Stream reach slope (%)	0.00	0.08	1.99	8.7
Catchment storage	Percentage of depositional areas (valley bottoms) in the catchment	0	17	75	9.0
Distance to river mouth	Minimum river distance of stream segment to mouth (Km)	50	352	762	12.4

Appendix 2. Freshwater fish species used for conservation prioritisation in the Daly River. Shown for each species are prevalence (proportion of 55 sites occupied) and predictive model performance in terms of correct classification rate (percentage of sites where the model correctly predicts species' presence-absence); model sensitivity (percentage of the sites where species' presence was correctly predicted); model specificity (percentage of the sites where species' absence was correctly predicted), and area under the receiver operating characteristic curve (AUC, see text and Fielding and Bell, 1997).

Species	**Common name**	**Prevalence**	**Correct Classification rate**	**Sensitivity**	**Specificity**	**AUC**
Megalopidae						
Megalops cyprinoides	Oxeye herring	0.20	0.66	0.18	0.77	0.51
Clupeidae						
Nematalosa erebi	Bony bream	0.42	0.75	0.70	0.78	0.71
Ariidae						
Neoarius berneyi	Berney's catfish	0.13	0.93	0.71	0.96	0.91
Neoarius graeffei	Blue catfish	0.22	0.89	0.75	0.93	0.86
Neoarius midgleyi	Shovel-nosed catfish	0.06	0.89	0.00	0.94	0.60
Plotosidae						
Anodontiglanis dahli	Toothless catfish	0.04	0.98	0.00	1.00	0.92
Neosilurus ater	Black catfish	0.47	0.75	0.73	0.76	0.78
Neosilurus hyrtlii	Hyrtl's tandan	0.56	0.56	0.61	0.50	0.61
Neosilurus pseudospinosus	False-spined catfish	0.11	0.82	0.17	0.90	0.65
Porochilus rendahli	Rendahl's catfish	0.15	0.82	0.38	0.89	0.65
Hemiramphidae						
Arramphus sclerolepis	Snub-nosed garfish	0.04	0.93	0.00	0.96	0.73
Belonidae						
Strongylura kreffti	Freshwater Longtom	0.29	0.82	0.69	0.87	0.85
Atherinidae						
Craterocephalus stercusmuscarum	Fly-specked hardyhead	0.35	0.78	0.68	0.83	0.77
Craterocephalus stramineus	Strawman	0.42	0.64	0.57	0.69	0.69
Melanotaeniidae						
Melanotaenia exquisita	Exquisite rainbowfish	0.11	0.96	0.83	0.98	0.96
Melanotaenia nigrans	Black-banded rainbowfish	0.06	0.93	0.33	0.96	0.85
Melanotaenia australis	Western rainbowfish	0.98	0.96	0.98	0.00	0.56
Pseudomugilidae						

Pseudomugil tenellus	Delicate blue-eye	0.06	0.93	0.33	0.96	0.95
Synbranchidae						
Ophisternon gutterale	Swamp eel	0.04	0.93	0.00	0.96	0.60
Chandidae						
Ambassis macleayi	Macleay's glassfish	0.13	0.86	0.43	0.92	0.75
Ambassis sp.	Northwest glassfish	0.51	0.53	0.54	0.52	0.63
Denaurisa bandata	Pennyfish	0.07	0.96	0.75	0.98	0.99
Centropomidae						
Lates calacrifer	Barramundi	0.42	0.76	0.74	0.78	0.80
Terapontidae						
Amniataba percoides	Barred grunter	0.67	0.78	0.84	0.67	0.80
Hephaestus fuliginosus	Black bream	0.64	0.64	0.71	0.50	0.67
Leiopotherapon unicolor	Spangled perch	0.93	0.89	0.94	0.25	0.79
Pingalla midgleyi	Midgley's grunter	0.06	0.96	0.67	0.98	0.85
Syncomystes butleri	Butler's grunter	0.27	0.58	0.20	0.73	0.54
Apogonidae						
Glossamia aprion	Mouth almighty	0.69	0.67	0.76	0.47	0.67
Toxotidae						
Toxotes chatareus	Seven-spot archerfish	0.40	0.71	0.64	0.76	0.77
Toxotes lorentzi	Primitive archerfish	0.07	0.86	0.00	0.92	0.51
Mugilidae						
Liza ordensis	Ord River mullet	0.26	0.96	0.93	0.98	0.95
Gobiidae						
Glossogobius aureus	Golden goby	0.56	0.71	0.74	0.67	0.74
Eleotridae						
Hypseleotris burrawayi	Katherine River gudgeon	0.06	0.96	0.67	0.98	0.85
Hypseleotris compressa	Empire gudgeon	0.11	0.80	0.00	0.90	0.75
Mogurnda mogurda	Northern trout gudgeon	0.73	0.71	0.80	0.47	0.70
Oxyeleotris lineolatus	Sleepy cod	0.51	0.56	0.57	0.56	0.58
Oxyeleotris selheimi	Giant gudgeon	0.80	0.82	0.89	0.55	0.66
Soleidae						
Leptachirus triramus	Freshwater sole	0.13	0.87	0.43	0.94	0.93
	Mean	**0.32**	**0.81**	**0.54**	**0.77**	**0.75**