Using water residency time to enhance spatio-temporal connectivity for conservation planning in seasonally dynamic freshwater ecosystems

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1 Summary

2 1. Addressing spatial connectivity in conservation planning is important to ensure the
3 maintenance of patterns and processes needed to support the persistence of biodiversity. In
4 freshwater ecosystems spatial connectivity is constrained by the presence of water, which
5 exhibits marked temporal changes in regions with wet-dry seasonal climates. Previous studies
6 have focused on spatial connectivity and overlooked the temporal component, which is
7 necessary to enable the functionality of spatial connections (due to temporal changes in water
8 availability).

9 2. We identify priority areas for the conservation of freshwater fish, water birds and turtles in
10 the Mitchell River catchment in the wet-dry tropics of northern Australia. We demonstrate
11 how adequacy of freshwater conservation can be enhanced by integrating an estimate of
12 water residency time (WRT) into the prioritization process. WRT reflects refugial potential
13 and connectivity in freshwater ecosystems and was quantified using MODIS flood and post-
14 flood Landsat satellite imagery. We compare the spatial allocation of priority areas, and the
15 spatial and temporal connectivity under two alternative scenarios: i) accounting only for
16 spatial connectivity and ii) integrating spatial and temporal connectivity.

17 3. Priority areas identified under the spatial and temporal connectivity scenario showed a
18 40% increase in WRT values with respect to the traditional spatial connectivity scenario. This
19 was achieved at no additional cost in terms of area required to be protected and maintaining
20 the same spatial connectivity.

21 4. Despite priority areas identified under the two alternative scenarios showing intermediate
22 spatial overlap (64%), the selection process was more efficiently biased towards planning
23 units with high WRT values. WRT in planning units that were only selected under the
24 temporal connectivity scenario was 2.5 higher than in planning units that only appeared in the

traditional connectivity scenario. This reveals the importance of accounting for WRT when identifying freshwater priority areas in wet-dry seasonal environments.

5. Synthesis and applications: Considering the temporal connectivity in conservation prioritization as we propose here helps to assess periods of longest spatial connections thereby maximizing the refugial role of freshwater priority areas during dry periods. When satellite imagery data and software publicly available our approach allows for an improved management of aquatic resources and biodiversity under periods of water scarcity that can increase in incidence and duration with climate change.

Keywords: climate change, lateral connectivity, longitudinal connectivity, Marxan, refuge, resilience.

Introduction

Connectivity is an important consideration in conservation planning to ensure the maintenance of the patterns and processes needed to support the long term persistence of biodiversity (Pressey *et al.* 2007). Hydrologic connectivity is a crucial determinant of ecosystem structure and functioning in freshwaters (Ward 1989; Pringle 2001; Hughes *et al.* 2009), and drives linkages among ecosystem elements in space and time (Fullerton *et al.* 2010). Hydrologic connectivity is featured in three spatial dimensions (Ward 1989): longitudinal (headwater-mouth), lateral (riverine-floodplain) and vertical (surface-ground water). This is critical for maintaining food web dynamics and ecosystem function at a range of spatial scales and the persistence of freshwater populations (Pringle 2001; Fausch *et al.* 2002; Bunn & Arthington 2002). For example, longitudinal fluxes of organic material are a distinctive feature of riverine food webs, with fluxes occurring between headwater streams, main channel reaches and estuaries. Hydrologic connectivity is also vital for the persistence of some species, such as diadromous fish that migrate long distances to complete their life cycles, or to allow re-colonization in seasonal systems after periodic low or high flow disturbances (Albanese *et al.* 2009).

The connected nature of freshwater ecosystems poses special challenges for effective conservation management, since human-caused disturbances in one area can seriously threaten freshwater biodiversity far away (e.g. upstream or downstream). For this reason, connectivity has been a focus of attention for freshwater conservation planning (Linke *et al.* 2011). Different approaches have been proposed to address longitudinal (Linke *et al.* 2007; Moilanen *et al.* 2008; Hermoso *et al.* 2011), lateral (Thieme *et al.* 2007; Ausseil *et al.* 2011; Hermoso *et al.* 2012) and vertical (Nel *et al.* 2011) components of connectivity. Despite these efforts, some aspects of connectivity have not been adequately accounted for in conservation planning approaches. In freshwater ecosystems, spatial connectivity, in all of its dimensions,

is limited by the presence of water, which is strongly influenced by temporal dynamics. In this way, functional connectivity (facilitation of movement of organisms through the landscape, *sensu* Taylor *et al.* 2006) is constrained by the presence of a minimum amount of water in the landscape (Fig. 1). This applies not only to obligate freshwater species restricted to movements within river networks, but also to organisms with aerial or terrestrial movements (e.g., spatial proximity of floodplain lakes, important for some birds and turtle species; Haigh *et al.* 1998; Rea *et al.* 2009). In climatic regions with pronounced wet to dry seasonality, such as the wet-dry tropics (Hamilton *et al.* 2002), or the Mediterranean (Gasith & Resh 1999), dry periods constrain the presence of water and the connections between the different elements of the system. Rivers and streams that are hydrologically connected during the wet season may cease to flow during the dry season and become reduced to a set of isolated pools. Important dry season refugia such as floodplain wetlands and lakes are also affected, becoming completely dry or constrained to a reduced area (Fig. 1). Water availability does not only fluctuate within annual hydrological cycles but also inter-annually, and extended dry periods (droughts) may periodically occur (Gasith & Resh, 1999; Bond *et al.* 2008). The frequency, duration and intensity of these events are expected to increase under the effects of climate change and some freshwater ecosystems that are currently perennial, will likely undergo more pronounced wet and dry cycles in the future (Bates *et al.* 2008).

Temporal changes in spatial connections can have important implications for population dynamics and community structure (Taylor *et al.* 2006) and ultimately for population viability (Magalhães *et al.* 2007). For example, connectivity can affect reproduction and mortality, by allowing or limiting access to potential breeding sites (Taylor *et al.* 2006). Incorporating the temporal dimension of connectivity (Pringle 2001) in freshwater

conservation planning is therefore a crucial challenge to adequately address the persistence of freshwater biodiversity (Nel *et al.* 2009).

Here, we demonstrate how to integrate a measure of Water Residency Time (WRT) in the landscape into previous considerations of spatial connectivity in conservation planning methods. We consider two different components of spatial connectivity: longitudinal connectivity within a catchment, and lateral connectivity between different sub-catchments. These types of connectivity were applied to address the spatial movement requirements of fish, turtles and waterbirds in the Mitchell River catchment (northern Queensland, Australia). In this way, we aimed to find a set of planning units that maintained water (i.e. to maximize the refugial role of freshwater priority areas) and allowed connections to be effective over the longest possible period of the hydrologic cycle to enable movement and access to key aquatic resources (functional connectivity). This novel approach to incorporating WRT in conservation planning methods would result in increased adequacy (capacity to maintain biodiversity over the long-term) of identified freshwater priority areas, and higher likelihood of future persistence of freshwater-dependent biota.

Methods

Study area

The Mitchell River catchment (71,630 km²) is located in northern Queensland, Australia (Fig. 2). The wet-dry tropical climate of the region is largely controlled by the equatorial southern monsoon. It is strongly seasonal with > 80% of the annual rainfall occurring between the wet season months of December to March (summer). Mean annual rainfall increases from around 600 mm in the south to over 1,200 mm in the northeast and northwest. High mean annual evapotranspiration leads to annual water deficits across the catchment except in the very wettest of years (Ward *et al.* 2011).

Biodiversity data

The spatial distribution of fish, water birds and turtle species was sourced from Kennard (2010). This database contained predictions of spatial distributions for 104 species of freshwater fish, 106 water bird species and 13 turtle species across northern Australia derived from Multivariate Adaptive Regression Splines models (Leathwick *et al.* 2005) at a fine scale (average area of predictive units was 3.6 km²). The predictive model was built on a data set of 1609 presence only sites plus 115 presence-absence sites and validated in an independent data set of 604 presence-absence sites for fish, and built and validated on 2109 and 350 presence-only sites for birds and turtles respectively (see Kennard 2010 and Hermoso *et al.* 2012 for more details on predictive models).

Identification of priority areas

We used the software Marxan (Ball *et al.* 2009) for identifying priority areas for conservation of freshwater fish, water birds and turtles. Marxan tries to find an optimum set of planning units that achieve the requested representation for each species (e.g., 100 km², hereafter termed conservation target) at the minimum cost. We used sub-catchments as planning units rather than equal-sized grid cells as usually done in terrestrial and marine conservation assessments. We delineated 2,316 planning units from a 9 second digital elevation model using ARC Hydro for ArcGIS 9.3 (ESRI 2002). We then translated the information from the predictive models for each of the 45 freshwater fish, 106 bird and five turtle species inhabiting the Mitchell River into the planning units by summing the area where each species was predicted to occur within each planning unit. Given the lack of ecological knowledge to guide more objective conservation target setting we set conservation targets to ensure the adequate representation of the rarest species in the dataset (the use of constant % targets for

all the species as usually done could lead to the underrepresentation of these rare species and overrepresentation of common ones). We adapted the target according to each species' prevalence in the dataset to represent 100% of the spatial distribution of the rarest species, and then scaled them down exponentially up to reach a minimum of 10% for the most common species. In this way the spatial distribution of rare species would be almost fully covered in solutions. To account for the importance of connectivity in freshwater conservation planning and the different requirements of the biodiversity that we were planning for, we incorporated two different types of spatial connections in the analyses. We used the longitudinal connectivity rule proposed in Hermoso *et al.* (2011) to account for the longitudinal propagation of threats and movements along the river network. Moreover, we incorporated inter-catchments connectivity (Hermoso *et al.* 2012), to account for movements of birds or turtles that are not necessarily restricted to movement via river networks (i.e. can move across drainage divides). We ran Marxan 100 times (1.5 M iterations each) to find 100 near-optimal solutions. The number of iterations per run was set after a sensitivity analysis to ensure convergence (measured as the average of planning units in the best solution) of the optimization algorithm. The solution with the lowest value for the objective function was used as the best solution in subsequent analyses. The frequency of occurrence of each planning unit across the 100 near optimal solutions was used as an estimate of their irreplaceability [the likelihood that an area will be required to meet a given set of targets, Pressey *et al.* (1994)].

Addressing temporal connectivity

We incorporated an estimate of water residency time (WRT) within each planning unit to represent spatial connectivity between planning units. In this way we aimed to maximize not only the spatial connection between planning units but also the time those connections

provided continuous aquatic habitat due to the presence of water. We used MODIS flood imagery (250 m resolution) (<http://modis.gsfc.nasa.gov/>), captured for February and March 2009, to map seasonal flood inundation extents, and post-flood Landsat TM 5 imagery (30 m resolution) (<http://landsat.usgs.gov/>), captured for March, June and October 2009, to map seasonal change in waterbody extents. A 20 year Landsat TM 5 dry season time series, captured in the late dry season in any year, was used to map dry season perennial waterbodies defined as being dry in less than 1 in 10 years (Environmental Protection Agency 2005). This resulted in a total of eight surface water extent snapshots in 2009, comprising four flood event snapshots, three dry season water extent snapshots, and one long term estimate of the extent of perennial water at the end of the dry season. The long term estimate of the extent of perennial waterbodies was included because cloud cover at the beginning of the wet season prevents image capture of water extent just prior to the onset of flooding. Although there is inter-annual variability in the magnitude of annual flood inundation in this region, the timing and duration of the wet season inundation and the dry season are highly regular in the study region (Kennard *et al.* 2010). We then summarized the information on the seasonal dynamics of surface water extents contained in grid cells for each planning unit. The main issue in doing this was how to capture the variability in WRT between planning units. Halls *et al.* (2008) propose a flood index based upon the sum of the number of days that a given lake area is flooded. We adapted this index as a measure of WRT, calculated as the surface water area-time integral, which measures the area under the curve of the relationship between surface water area and time it remains for each planning unit (Fig. 3). The measure of WRT used here was estimated using the trapezoidal rule (Atkinson 1989). The resulting WRT unit is area-time (e.g. hectare-days). A consequence of WRT calculated in this way is that the same area-time integral value can be obtained for a small amount of water that resides in a planning unit for a long time as well as for a large amount of water that resides for a short time. To

186 address this issue, the surface water area-time integral used to calculate WRT was weighted
187 by the proportion of time water resides in the planning unit. For each planning unit, the
188 weight is calculated as t_i/T where t_i is the time from the beginning of the time series to the i th
189 surface water area measurement, and T is the total length of the time series.

190 We then used the WRT to weight the spatial (longitudinal and inter-subcatchment)
191 connections in Marxan. The longitudinal connectivity penalty accounts for connections along
192 the river network using a distance-decay function, so for example, the penalty for not
193 including a planning unit located far upstream of a selected one would be lower than if not
194 including the most immediate upstream (Hermoso *et al.* 2011). The inter-subcatchment
195 connectivity penalty incorporates connections not included in the upstream-downstream
196 topology. This additional component of connectivity was recently incorporated to freshwater
197 conservation planning to account for the ecological needs of not strictly water dependent
198 freshwater taxa (e.g., waterbirds and some turtles that can move across the landscape;
199 Hermoso *et al.* 2012). We multiplied the connectivity penalty described in Hermoso *et al.*
200 (2011; 2012) by the minimum WRT for the pair of planning units involved in every
201 connection (Fig. 4). In this way, if two planning units were spatially close but retained water
202 only for a few weeks a year, a low penalty would apply (the spatial connection is very
203 ephemeral and is therefore not considered as important). On the other hand, close planning
204 units that retained water most of the year offered a high temporal-spatial connection. Given
205 the difference in magnitude between the spatial penalties and WRT (Fig. 2), we used a log
206 transformed WRT to weight the spatial connectivity penalty. In this way we ensured that we
207 optimized for both, spatial and temporal connectivity, at the same time.

208 To test the effect of WRT, we identified priority areas for conservation of freshwater
209 biodiversity in the Mitchell River catchment under two different scenarios, with and without

WRT-weighted spatial connectivity. We used each planning unit's area as a surrogate of cost in the analyses.

We measured the total length (kilometres) of connected planning units within the best solution and the average WRT of planning units within and outside the best solution in both scenarios (with and without WRT) and for 100 best solutions randomly generated (random allocation of the same number of planning units across the study area). We also estimated the potential overall benefit of WRT to species represented in the best solution by measuring the WRT in selected planning units where each species occurred. In this way we had an estimate of WRT in priority areas where each species was expected to be present. We then checked for significant differences in the average WRT of planning units in the best solution and the species' WRT benefit (with vs. without WRT) by means of a one-way ANOVA. A conceptual diagram of the analyses performed can be found in Figure S1 in Supporting Information.

Results

The spatial allocation of best solutions and highly irreplaceable areas in the Mitchell River catchment was influenced by the incorporation of WRT (Fig. 5). Both solutions could be taken as reasonable priority areas as conservation targets were fully achieved in both cases. There was an intermediate overlap between both solutions with 64% of planning units (n=165) selected in both scenarios. Despite this coincidence, the use of temporal connectivity had a significant effect in the selection of planning units. Planning units that were selected only under the temporal scenario (n=52) showed WRT values 2.5 higher (average WRT=4200) than planning units only selected under the traditional connectivity scenario (n=40 planning units, average WRT=1712). This was also reflected in the change of spatial patterns of irreplaceability (Fig. 5). High irreplaceable areas shifted from intermediate

reaches to lowland reaches where WRT showed higher values on average (Fig. 2). There was a substantial difference in temporal connectivity between both scenarios (Fig. 6). The average WRT value for planning units included in the best solution when using WRT was higher (40% increase on average) than when it was not used (Fig. 6). The difference in spatial allocation of priority areas when using WRT did not affect either the degree of spatial aggregation of priority areas, the total area required or the achievement of conservation goals (all the species achieved the required target in all cases). In both cases the average fully spatially connected river length within priority areas was around 322 km for each patch of clustered planning units and the total area required was around 8000 km² (Fig. 5, Supplementary Table S1). Note that the total number of planning units included in the best solutions was similar with and without WRT (n= 205 and n=216, respectively) and therefore unlikely to influence our assessment of the benefits of incorporating WRT. The preferential selection of planning units with high WRT in the best solution also translated into an increase in WRT where each species occurred within best solutions (Fig. 7). The average species WRT benefit was significantly higher when using WRT (ANOVA, $F_{(1,304)} = 48.3$, $P < 0.001$). See Table S1 in Supporting Information for a summary of results of comparisons between scenarios.

Discussion

There is increasing concern among conservation practitioners to quantify and manage processes that support the persistence and functioning of ecosystems and their biodiversity (Meir *et al.* 2004, Possingham *et al.* 2005; Pressey *et al.* 2007). Here, we have demonstrated how to integrate an estimate of WRT in the identification of priority areas for conservation to enhance the management of biodiversity. We have addressed two important features of aquatic ecosystems to improve adequacy of freshwater priority areas, namely the seasonality

of spatial connectivity, and the presence of dry-season refuges. This will help maintain some key ecological processes such as persistence and movements of biota over the dry season or re-colonization when water returns, which are essential factors to secure the long-term maintenance of freshwater biodiversity.

Native biodiversity in dynamic wet-dry seasonal freshwater environments have developed strategies (desiccation resistant life-history stages or retreating to refuge habitats, fast recolonisation and recruitment after disturbance) to cope with extended dry periods (Bond *et al.* 2008). For example, Magalhães *et al.* (2007) found that fish assemblages in Mediterranean streams recovered quickly from short-term fluctuations in water level. However, they also warned that exacerbated disruptions in longitudinal connectivity caused by low water levels could negatively influence sensitive species. This is especially concerning under the expected effects of climate change on water availability (Bates *et al.* 2008). Global-scaled predictions include a 2–3 fold increase in the frequency of extreme low flows in many areas (Arnell 2003) and a reduction in mean annual discharge. Under these conditions, it is likely that some currently perennial freshwater ecosystems will become non-perennial and that the duration and extent of water scarcity in already wet-dry seasonal ecosystems will increase. This represents a challenge for conservation of freshwater biodiversity, since the new conditions will affect ecosystem functioning and might surpass some species' ability to adjust or adapt to these changes (Morrongiello *et al.* 2011).

Focusing conservation efforts in those areas that retain water and allow connections for long periods of time is an appropriate strategy to improve long-term persistence of freshwater-dependent biota. Here, we demonstrated a substantial increase in WRT within priority areas (40%) without no additional increase in area selected and maintaining the spatial connectivity constant (both scenarios showed similar number of planning units and length of river connected in the best solution). In this way we focused the selection of priority areas in more

perennial areas where freshwater biodiversity has a higher chance of resisting the dry period. There was a shift in the spatial allocation of irreplaceable areas when introducing WRT in the selection process. When using WRT to weight spatial connections, the selection of priority areas was focused on those zones that enabled movements along the river network (longitudinal connectivity, Hermoso *et al.* 2011) and between floodplain wetlands and lakes (inter-subcatchments connectivity, Hermoso *et al.* 2011) for a longer period of time. This result should satisfy seasonal connectivity requirements for a range of different species, such as waterbirds and turtles between wetlands and lakes that maintained water or fish within river reaches where water levels provided functional connections. By incorporating WRT in the identification of priority areas we focus attention on areas that help not only to enhance biodiversity persistence by increasing the connectivity potential for biota within priority areas, it also provides relevant information regarding assisted translocations of sensitive biodiversity elements that otherwise face impassable migration barriers within and across catchments. This in turn, can promote resilience of freshwater biodiversity elements that are sensitive to increased frequencies and durations of droughts associated with a changing climate by focusing conservation efforts on potential refuge areas. This is an important feature in wet-dry seasonal ecosystems like those in the Mitchell River catchment in northern Australia. This catchment features a high mean annual rainfall and high evapotranspiration, which often leads to annual water deficits in some parts of the catchment. For example, a post-flood surface water contraction of 89% in area has been recorded between March and October in 2009 (D. Ward unpublished data). Seasonality in water availability was spatially heterogeneous with a pattern of increasing WRTs towards lower reaches of the Mitchell floodplain. Perennial aquatic habitats in these parts of the catchment function as biological refuges during dry periods and as re-colonisation sources at the onset of flooding at the beginning of the next wet season (Magoulick & Kobza 2003).

Priority areas identified in our study hold water for most of the dry period allowing species to have access to key resources when they are scarce (e.g., some waterbirds or turtles; Haigh *et al.* 1998; Rea *et al.* 2009) and offer refugial opportunity (e.g., freshwater fish; Arthington *et al.* 2005). This should help address the ecological needs of some species and sustain populations that will eventually serve as sources of colonization when water returns water returns. The potential recolonisation from refuge areas might be compromised by the presence of barrier to the movement especially for water strict species (e.g., dams). Although this was not a major issue in our study area we acknowledge that it should be further considered when estimating the potential benefit of a given refuge area in other catchments where barriers constraint biota movements.

The method proposed here is transferable and could be used to address adequacy in freshwater conservation planning in regions of the world subject to strong seasonality in water availability. Satellite imagery and the software Marxan used in this work are publicly available, which could facilitate the application of the method we demonstrate here.

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Supporting Information

335 Additional Supporting Information may be found in the online version of this article:

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337 Table S1. Summary of comparison between scenarios.

338 Fig. S1. Conceptual diagram of analyses.

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Fig. 1. Change in water level and connectivity potential across a hydrologic cycle for a perennial and a seasonal (dotted line) water body. Perennial water bodies offer refuge to freshwater biota for longer periods of time (t') than seasonal waterbodies (t), and allow movements for longer periods (the minimum water level to allow connections remains for most of the hydrological cycle). Lines on top of the figure represent the extent in time in the two water bodies.

Fig. 2. Location of the Mitchell River catchment in northern Australia and Water Residency Time (WRT) for each of the 2,316 planning units used in this work. WRT was calculated as shown in Fig. 3.

Fig. 3. Dynamics of Water Residence Time (WRT) in planning units with short and long WRTs (left and right figures respectively). WRT is calculated as the area under the curve of the relationship between surface water area and the time it remains for each planning unit.

Fig. 4. Examples of how the connectivity penalty (indicated by arrow thickness) was calculated by combining information on water residency time (WRT, indicated by shading on the river network) and spatial connectivity (longitudinal and inter-subcatchment combined). High connectivity penalties would apply if two close planning units that maintain water for most of the year are not selected at the same time. This penalty decays with distance between planning units (either longitudinal or inter-subcatchment) and time they do not maintain water.

Fig. 5. Best solutions and irreplaceability values for two planning scenarios: with and without Water Residency Times (WRT) as weight to spatial connection.

Fig. 6. a) Mean ($\pm$ SE) Water Residency Time (WRT) within high priority areas (planning units selected in best solution) and low priority areas (not selected) for three different scenarios: planning with no WRT considerations, using WRT to weight spatial connectivity, and random selection of planning units (100 solutions containing 200 planning units). b)

486 Water Residency Time (WRT) for planning units where each species occurred within the best
487 solution (mean $\pm$ SE across species) under the two scenarios tested in this work (with and
488 without WRT as a weight to spatial connections).

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490 Figure 1.

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Figure 4.

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