Spatiotemporal dynamics of surface water networks across a global biodiversity hotspot—implications for conservation

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Abstract
The concept of habitat networks represents an important tool for landscape conservation and management at regional scales. Previous studies simulated degradation of temporally fixed networks but few quantified the change in network connectivity from disintegration of key features that undergo naturally occurring spatiotemporal dynamics. This is particularly of concern for aquatic systems, which typically show high natural spatiotemporal variability. Here we focused on the Swan Coastal Plain, a bioregion that encompasses a global biodiversity hotspot in Australia with over 1500 water bodies of high biodiversity. Using graph theory, we conducted a temporal analysis of water body connectivity over 13 years of variable climate. We derived large networks of surface water bodies using Landsat data (1999–2011). We generated an ensemble of 278 potential networks at three dispersal distances approximating the maximum dispersal distance of different water dependent organisms. We assessed network connectivity through several network topology metrics and quantified the resilience of the network topology during wet and dry phases. We identified ‘stepping stone’ water bodies across time and compared our networks with theoretical network models with known properties. Results showed a highly dynamic seasonal pattern of variability in network topology metrics. A decline in connectivity over the 13 years was noted with potential negative consequences for species with limited dispersal capacity. The networks described here resemble theoretical scale-free models, also known as ‘rich get richer’ algorithm. The ‘stepping stone’ water bodies are located in the area around the Peel-Harvey Estuary, a Ramsar listed site, and some are located in a national park. Our results describe a powerful approach that can be implemented when assessing the connectivity for a particular organism with known dispersal distance. The approach of identifying the surface water bodies that act as ‘stepping stone’ over time may help prioritize surface water bodies that are essential for maintaining regional scale connectivity.

Keywords: surface water dynamics, spatiotemporal dynamics of surface water networks, complex networks, graph theory, remote sensing, Landsat, conservation

Introduction
Aquatic systems, and their biota, are some of the most threatened ecosystems in the world (Saunders et al 2002, Nel et al 2009) since they are affected by changes in climate and anthropogenic factors (e.g., land use change in the
catchment). These factors not only increase direct stress on surface water habitat but also affect dispersal opportunities for water dependent organisms as neighbouring water bodies degenerate. Moreover, most water dependent organisms, defined here as vertebrates (e.g., amphibians or waterbirds) that either live in water bodies or are dependent on water bodies for critical periods during their life stages, live in metapopulations and travel between water bodies to maintain sustainable and resilient populations. Thus adaptations to climate change at regional and landscape scales require measures that facilitate species dispersal such as preserving or enhancing landscape features essential for species connectivity.

Graph theory, a branch of mathematics useful for describing how objects are connected in space (e.g., social networks, World Wide Web, road networks), is a powerful approach for assessing connectivity (Urban and Keitt 2001, Calabrese and Fagan 2004, Minor and Urban 2008) with valuable applications in ecology, social sciences, and physical systems (Strogatz 2001, Borgatti et al 2009, Olesen et al 2011). Networks in ecology are based on graph theory and are comprised of a set of nodes (vertices), which can have properties such as location and size, and the relationships between these nodes, represented via edges. Given their capacity for describing conservation and management systems at regional scales, networks have become powerful tools in spatial ecology (Bunn et al 2000, Urban and Keitt 2001, Fagan 2002). Spatial graphs have been successfully applied in terrestrial ecology (Urban et al 2009) and more recently in marine conservation (Treml et al 2008). Wetland connectivity has also been a focus for graph theory but limited to few small-scale snapshots in time (Fortuna et al 2006, Wright 2010).

Most studies assumed a fixed network structure through time, which is particularly of concern for aquatic systems that typically show high natural variability in space and time (Puckridge et al 1988). For example, variability in the node set is likely to have substantial implications for the size and density of the resulting network and subsequently on the behaviour and properties of networks. Failing to consider the temporal dynamics in a network can lead to spurious results for the system under investigation (Butts 2009). Acknowledging the importance of representing the high spatiotemporal dynamics in network structure, previous studies have modelled the response of habitat networks to removal of habitat patches either randomly (Urban and Keitt 2001) or based on anticipated changes such as wetland drying (Fortuna et al 2006), or as snapshots in time of how wetland networks change during a drought, deluge or an average rainfall year (Wright 2010). Yet, the actual dynamics across space and time using time series data of surface water body networks can only be accomplished by employing seasonally continuous time series of surface water bodies derived from remote sensing data and linking these with network analysis (Wright 2010). There has been little progress in understanding the actual effects of loss of habitat using time-series of remotely sensed data as connectivity networks change in space and time. Here we determined past patterns of surface water body connectivity integrating graph theory with a 13 year seasonally-continuous time series of remotely sensed surface water bodies.

Patterns of connectivity are assessed through knowledge of network topology and associated metrics and how these change over time (e.g., number of edges, number of clusters, average path length, table 1). Importantly this provides insight into emergent network properties, such as the spread of information and network resilience and vulnerability to

### Table 1. Description of network connectivity metrics computed for seasonally continuous network time series on the Swan Coastal Plain from 1999 to 2011.

| Metrics used in the connectivity analysis | Definition | Ecological meaning | Citation |
|------------------------------------------|------------|--------------------|----------|
| Number of edges                          | Total number of edges in a network given the search radius | Connectivity among habitats | (Newman 2003) |
| Number of clusters                       | Counts the numbers of disconnected sub-graphs | Potential discrete populations | (Newman 2003) |
| Average minimum path length              | Average number of edges in the shortest path between all pairs in a graph averaged over possible between-vertex connexions | How quick creatures can disperse across the entire system | (Montoya and Sole 2002) |
| Diameter                                 | Longest minimum path length that exists between any nodes in a network | The number of dispersal events to reach any part of the system | (Montoya and Sole 2002) |
| Transitivity/clustering coefficient       | How clustered nodes are | Average local resilience based on a supporting triangular linkage structure | (Montoya and Sole 2002) |
| Average betweenness centrality—nodes     | Average proportion of shortest paths going through a vertex | Calculates shortest paths and based on a count of the paths passing through each node a proportion is calculated. This can represent ‘stepping stones’ if the assumption that those animals chose the shortest path is accepted. | (Newman 2003) |
disturbances (Melián and Bascompte 2002). Based on topology, several types of networks can be identified. These networks include planar, regular, random and complex (e.g., small-world and scale-free). For planar networks, no edges cross or intersect and have long average path length and low clustering coefficient (Minor and Urban 2008). This would be applicable to a dispersing organism that moves only small distances to neighbouring habitats. Random networks have a bell-shaped degree distribution highlighting that most nodes have a similar number of edges, with an absence of network hubs. Most ‘real world’, networks are not represented by random configurations. One common network type is a power-law or scale-free distribution, where edges connect based on preferential attachment also known as the ‘rich get richer’ algorithm. The resultant network has the majority of nodes having a minimal number of links and a few nodes having a very high number of links (Newman 2003). These networks have short path lengths and are resilient to random attack but vulnerable to targeted attack of the hubs. Examples of systems that can be modelled with this network configuration include the World Wide Web, the citation network and wetlands of the prairie pothole in North America (Wright 2010). A small-world network is similar to a scale-free distribution but it is highly clustered, has more shortcuts and shorter average path lengths (Watts and Strogatz 1998). Examples of these configurations include neural networks, evolving networks and the Great Barrier Reef (Kininmonth et al. 2010). Comparing existing networks with simulated network models of known topology and properties is important because it provides insight into regional and emergent network properties and allows us to make inferences about habitat connectivity and thus conservation strategies.

Besides assessing the temporal dynamics in connectivity and the resemblance with theoretical network models, changes in network topology metrics following structural disturbance allows us to quantify network resilience. Knowledge of network resilience provides understanding of how landscape connectivity might change as a function of an ‘attack’ to the network (e.g., small surface water body removal as they dry out due to a warmer climate). At the landscape scale, network models are useful for linking species movement among habitat patches (Keitt 2003) and quantifying the survival of metapopulations under habitat loss by identifying ‘stepping stone’ patches (Urban and Keitt 2001, Keitt 2003). ‘Stepping stone’ patches act as connectivity ‘bottlenecks’ enabling access to multiple habitats because of their position in the landscape. Because ‘stepping stone’ water bodies are critical linkages in surface water networks, identifying them across space and time provides important information for prioritizing surface water bodies in need of conservation.

Here we focused on a global biodiversity hotspot in Western Australia and conducted a temporal analysis of water body connectivity over 13 years of variable climate using graph theory. Specific objectives addressed in this research were to:

1. Assess changes in connectivity over time and examine the impact of climate variability in this system using a range of network topology metrics.
2. Assess the resilience of the surface water networks by quantifying the impact of removing nodes on network topology according to four different strategies (removing smallest, random, least and most connected nodes) during a wet and a dry time phase.
3. Identify ‘stepping stone’ surface water bodies across space and time.
4. Compare with other constructed networks and assess whether networks are similar to constructed random, scale-free or small-world networks.

Methods

Study site and data used

Our study site was the Swan Coastal Plain (SCP), a 36000 km² area that encompasses one of the 25 global biodiversity hotspots (sensu Myers), defined as biogeographic regions that contain at least 0.5% or 1500 of the world’s 300 000 endemics plant species and have lost 70% or more of their primary vegetation (Myers et al. 2000). The SCP has over 1500 wetlands that retain significant biodiversity values with several listed as protected wetlands of international importance under the Ramsar convention while others are recognized as nature reserves and wetlands of national importance (Davis and Froend 1999). However, more than 70% of the wetlands have been lost since European settlement and the SCP is an area affected by recent drying climate and rapid urban development and ground water abstraction. The SCP shows high seasonal and inter-annual variability in surface water dynamics (Tulbure and Broich 2013a), with winter filling and summer drawdown (Townley et al. 1993).

We used the seasonally continuous Landsat archive to derive an ensemble of 278 potential surface water body networks for the SCP. The data covered a period spanning 13 years when the SCP experienced one of the driest years on record (Bureau of Meteorology 2011), representing a unique opportunity to study how the networks change during extreme climatic events. Surface water dynamics data have been developed using the Landsat TM and ETM+ imagery for the SCP from 1999 to 2011 (Tulbure and Broich 2013a). The overall classification accuracy of surface water bodies was 96% (with 89% producer’s accuracy and 93% user’s accuracy) and yielded 278 surface water time steps, each corresponding with a Landsat acquisition over the study area. The data are freely available (Tulbure and Broich 2013b) and an animation of the dynamics is available at the following link: http://www.mirela-tulbure.com/surface-water-dynamics/.

Tulbure and Broich (2013a) showed that the number, total area and size of water bodies have considerable intra and interannual variation with highest values in winter and lowest values in the Southern hemisphere summer. To reduce the
analytical artifacts in the surface water data, the 900 m² water bodies (single Landsat pixel water bodies with no neighbouring water pixel) were removed. We computed the area of each water body polygon for every time step. We assigned a unique identifier to temporally overlapping polygons. For each water body, we first determined the maximum extent during the 278 time steps and assigned it a unique identifier. Any overlapping polygons across the time series were assigned the same identifier to ensure that in years when water bodies shrink or split into smaller water bodies they were identified and tracked in subsequent analyses as part of a seasonally larger water body.

The dispersal ability of water dependent biota is highly variable and results in diverse temporal and spatial patterns of connectivity (Morris 2012). Landscape connectivity is species specific and varies across scales. Rather than focusing on one particular organism, here we focused on how the landscape scale connectivity of the entire biogeoregion changes from the perspective of a range of water-dependent organisms with different dispersal distances, aiming to generalize the results. To create potential networks we used three example dispersal distances (500 m, 1000 m and 2000 m) approximating a wide range of water dependent species (Smith and Green 2005). Dispersal distances considered here approximate dispersal of amphibian species and turtles as well as waterbirds during breeding and moulting when they need close proximity to water bodies (Roe and Georges 2007, Morris 2012). Pairwise distances between water bodies were computed as Euclidian distances between the nearest edges under the assumption that the habitat matrix is homogeneous (Urban and Keitt 2001). The edge weights, representing a cost of movement, were simplified to be directly proportional to dispersal distances. The network was assembled based on unique water bodies as nodes.

Climate data

We used monthly spatially explicit climate data from the Australian Water Availability Project (Raupach et al 2009, 2011). For climate variables we selected precipitation and maximum, minimum and average temperature in the same months as the image acquisition. To investigate lag time effects we also used the climate variables in the previous month, including the average of the previous two, three and four months from the image acquisition date. We conducted cross-correlations between the number of water bodies against climate variables and picked a precipitation and a temperature variable based on the highest linear correlation values. Next section provides methodology specific to each of the four objectives.

(1) Connectivity over time

For connectivity analysis we used the igraph package (Csardi and Nepusz 2006) in the statistical R software (R Development Core Team 2012) to compute several network topology metrics (Newman 2003). Network topology metrics included number of edges (links between water bodies), average path lengths of a graph, transitivity (graph-wide average clustering coefficient) and diameter (Urban and Keitt 2001, Urban et al 2009) and are summarized in table 1. For a more in depth description of network topology metrics readers are referred to Newman (2003).

We used Mann–Kendal statistics to assess the temporal trend of network topology metrics over the 13-year time series. We first assessed whether the autocorrelation in each data series was significant using the acf function in the Kendall package (McLeod 2011). If there was a significant autocorrelation in the data set we used the Mann–Kendall modified trend test for serially correlated data in the fume package (Group 2012) and noted the p-value for significance.

(2) Network resilience

We tested how the network topology responds to loss of nodes and contrasted the network response to node removal during a wet (July 2005) and a dry time step (December 2010) at a dispersal distance of 2000 m. These two time steps were chosen to correspond to one of the wettest and driest times steps with the highest and lowest number of nodes, respectively. Using these contrasting wet and dry time steps, we removed nodes (water bodies) in 1% increments from 1 to 30% based on four different strategies. The four strategies included the removal of nodes based on size (based on calculated area), random selection, least connected (lowest degree) and highest connected. We considered the impact of these removals on several topology metrics which included number of edges, number of clusters, diameter relative to number of nodes, average path length relative to number of nodes and transitivity.

(3) ‘Stepping stone’ water bodies

To assess which surface water bodies acted as ‘stepping stone’ over time and at three maximum dispersal distances we computed average betweenness centrality per ‘unique’ water body per time step (definition of unique below). The analysis was complicated by the seasonal dynamics with wet winters and dry summers as well as the drying trend between 1999 and 2013. During the wet winter, water bodies expand and several small water bodies can merge into a larger water body. Conversely, during the summer certain larger water bodies disintegrate into multiple smaller ones, some of which persist to the next wet season while others dry up and subsequently refill during the next wet season. In order to identify ‘stepping stone’ nodes in the network, small water bodies that merge into a larger water body were treated as a single water body. For this purpose we used a ‘unique’ identifier (based on the maximum extent of the water body) to track and treat as ‘unique’ water bodies that broke up, overlapped and reunited over time. After computing betweenness per ‘unique’ water body per time step, we then took the average betweenness of each unique water body for the entire time series. This allowed us to rank water bodies based on their betweenness centrality over the time series.

(4) Comparison with other networks

We compared our 278 surface water networks with four theoretical networks (random, scale-free and two small-world networks) using the same number of nodes and when possible the same average degree with our surface water body networks. The theoretical networks included (1) the random Erdos–Renyi network, which uses the same number of nodes.
and edges, adding edges chosen uniformly randomly from all
the possible edges (Erdős and Rényi 1959); (2) the scale-free
Barabási–Albert model, whereby one vertex is added at each
time and edges are then created to link nodes following
preferential attachment based on degree distribution (Barabási
and Albert 1999); (3) the Watts–Strogatz small-world model,
where first a regular lattice is created and then edges rewired
uniformly with a specified probability (Watts and Stro-
gatz 1998); (4) small-world ‘forest fire’ network, which
resembles a forest fire spreading by igniting trees close by,
and where nodes are added sequentially and edges are created
based on existing configuration (Leskovec et al 2007).

At each of our 278 time steps across 13 years, we
computed the average path length and the clustering co-
efficient of our networks as they are indicators of network type
and compared them with the average path lengths and clus-
tering coefficient of the four constructed networks.

Results

(1) Temporal variability in connectivity

Topology metrics of surface water networks at different
maximum dispersal distances varied by an order of magni-
itude. All network topology metrics computed (e.g., number
of edges, number of clusters, diameter and average path length
as well as global transitivity) showed a highly dynamic sea-
sonal variability (figure 1). A significant decline over time can
be noted at all three dispersal distances ($p < 0.001$) for the
number of edges (figure 1(a)) and number of clusters
(figure 1(b)). It is important to note that the lowest number of
clusters (CI = 110) was in 2010, which was an unusually dry
year, after which the range of seasonal variability was
reduced. The average path length and diameter relative to
number of nodes showed seasonal variability and an
increasing trend over time at all three distances (figures 1(c)
and (d)). This suggests that dispersing through these networks
would take more energy if the drying trend continues. The
clustering coefficient stayed relatively similar over time at
1000 m and 500 m dispersal distances but slightly increased at
2000 m (figure 1(e)).

Average precipitation in the previous two months to
image acquisition explained the highest proportion (70%) of
variability in number of nodes and had a positive relationship
with number of nodes (F-statistic = 626.3, df = 272,
$p < 0.001$). Maximum temperature in the previous month
explained the highest proportion (65%) of variability in
number of nodes and the relationship with number of nodes
was negative (F-statistic = 501.9, df = 272, $p < 0.001$).

(2) Network resilience

We removed nodes from the network during two con-
trasting (wet and dry) time steps at a dispersal distance of
2000 m and based on four different strategies (smallest, ran-
dom, least and most connected nodes) and recorded the
impact on several network topology metrics (number of edges
and clusters, diameter relative to number of nodes, average
path length relative to number of nodes and transitivity). The
overall trends in network topology metrics as a response to
node removal were similar between the dry and wet time
steps. During the dry time step, the total number of nodes
removed varied between 6 and 193 nodes which corre-
ponded to 1% and 30% respectively from a network with
644 nodes. The wet time step investigated here was among
the time steps with the highest number of water bodies
($N = 3147$) and the number of nodes removed representing 1
and 30% of the nodes varied between 31 and 994,
respectively.

The total number of edges in the observed networks
increased over time for all four removal strategies, however
as expected, it decreased fastest when removing the highly
connected nodes (measured by the degree) and lowest when
removing the least connected nodes, while the smallest area
and random removal showed more similar results
(figure 2(a)). The number of clusters showed a slight decrease
when removing the smallest nodes and when removing nodes
randomly (figure 2(b), figures 3(b) and (c)). In contrast, the
number of clusters increased when removing the most con-
nected nodes and decreased when removing the least con-
nected nodes (figure 2(b)). The diameter and average path
length, normalized over the network size, increased over time
for both wet and dry time steps for all node removal strategies
with the exception of the highly connected node removal
which initially increased up to 10% node removal and then
decrease until 30% node removal for the dry time step
(figures 2(c) Dry and 2(d) Dry). For the wet time step, the
diameter and average path length normalized over the net-
work size increased up to 20% and then decreased after that
(figures 2(c) (d) Wet panel). Transitivity or the clustering
coefficient remained similar for all except the highly con-
nected node removal strategy which showed an increase in the
clustering coefficient (figure 2(e)). Despite the fact that the
overall trends in network topology metrics as a response to
node removal were similar between the dry and wet time
steps, the original networks were different during dry and wet
phases (figure 3(a)). Networks during dry and wet time steps
were also visually different under the four different removal
strategies (figures 3(b)–(e)).

(3) ‘Stepping stone’ water bodies

We computed average betweenness centrality over the 13
year period for each water body at three dispersal distances
to assess which water bodies act consistently as ‘stepping stone’
and whether they are functionally similar at different dispersal
distances. At all three dispersal distances water bodies with
high betweenness centrality were located in the area sur-
rounding the Peel-Harvey Estuary, primarily South and West
of the estuary. At 2000 m the water bodies with the highest
betweeness centrality included the large lakes South of the
Peel, such as Preston Lake, Lake Clifton, Lake Newnham,
Lakes Hayward, Yalgorup, Martins Tank Lake as well as
Black Swan Lake (figure 4(a)). Several of these lakes were
important as stepping stones at a 1000 m dispersal distance
with the expection of Lake Preston and Martins Tank Lake and
Lakes Yalgorup and Hayward (figure 4(b)). At 500 m the
water bodies with highest betweenness centrality included
smaller water bodies (figure 4(c)) located primarily East of the
Peel-Harvey.
Comparison with theoretical networks

To assess which theoretical network model they resemble the most, we compared differences in clustering coefficient and average path length between the time-series of SCP surface-water networks with existing random, scale-free and small-world models at three distances. The surface water networks derived in this work had similar clustering coefficient to the forest fire small-world network at 2000 m but a lower clustering coefficient than the small-world Watts–Strogatz networks and had similar average path lengths to the small-world Watts–Strogatz networks (figure 5(a)). The networks were more clustered than the random network and scale-free network (figure 5(a)), suggesting that at 2000 m the networks are closest to a small-world network. At both 1000 m and 500 m the networks were less clustered than the small-world networks and more similar to the scale-free networks. The network had longer average path lengths at 1000 m than the scale-free network (figure 5(b)) and showed more temporal variability in both the average path lengths and clustering coefficient than the scale-free at 500 m (figure 5(c)).

Figure 1. Graph theory metrics for the Swan Coastal Plain from 1999 to 2011 (278 time steps) at three different dispersal distances 2000 m (left columns; red), 1000 m (middle column; green) and 500 m (right hand column; blue) over time (x-axis shows the 278 time steps). Connectivity metrics include (a) number of edges, (b) number of clusters, (c) relative average path length (average path length divided by the number of nodes), (d) relative diameter (diameter divided by the number of nodes), and (e) transitivity. P-values are <0.001 except for the last two graphs where P-values = 0.65 and represent significance of the temporal trend line (see method for explanation).

Discussion

Our work quantified dynamics in landscape connectivity through the integration of a seasonally continuous time-series of surface water bodies derived using the entire USGS Landsat archive over the study area from 1999 until 2011 and an ensemble of potential networks derived using graph theory. We focused on an area that encompasses one of the world’s 25 global biodiversity hotspots, where the majority of surface water bodies have been lost (Horwitz et al 2008, Froend and Sommer 2010). We identified and quantified changes in landscape connectivity as the rainfall patterns vary across extended ranges of time of over a decade leading to high dynamics in water body extent, numbers and subsequently network connectivity metrics.
Figure 2. Changes in the graph theory metrics ((a) number of edges, (b) number of clusters, (c) diameter relative to number of nodes, (d) average path length relative to the number of nodes and (e) transitivity) for surface water bodies on the Swan Coastal Plain in a dry phase (December 2010, left panels) and during a wet phase (July 2005, right panels) when removing nodes based on four different strategies at a dispersal distance of 2000 m. The four removal strategies were smallest nodes removed first (red line), random removal (green), least connected nodes (blue line) and most connected nodes (black line) and removed nodes in increments of 1% from 1 to 30% nodes in a network.
We computed several network topology indices for the SCP surface water body networks to characterize changes in connectivity from 1999 to 2011. Results suggest that since 1999 the surface water networks, at the three examined dispersal distances, have increased in diameter and average path length. Whereas other connectivity metrics suggest that over time there were fewer clusters of connected water bodies and fewer links between water bodies. As groups of surface water bodies are a more meaningful unit of management and conservation than individual lakes (Johnson et al. 2010), these results point to the fact that the connectivity has significantly decreased since 1999 until 2011, with potentially negative consequences for species that have limited dispersal capacity (e.g., amphibians). An aquatic organism would have fewer opportunities for dispersal events (implying the need for more time and effort) to connect to the spatially distributed individuals of the same species. Long term implications for metapopulation viability are likely given this decadal trend of decreasing connectivity. We assessed the impact of climate variability on network topology metrics and found that average precipitation in the previous two months explained approximately two third of the variability in number of nodes. Future work should use downscaled global climate models to forecast changes in surface water structure under various climate change scenarios and help prioritize surface water bodies in need of conservation for maintaining regional scale connectivity for different groups of organisms.

We assessed the resilience of the network by quantifying the impact of node removal on several network topology metrics. Assuming that the smallest water bodies would dry out first in a drier climate and given that the size of water bodies and depth are correlated (Halse et al. 1993), we removed nodes according to four different strategies including removing smallest, randomly, least and most connected nodes. Removing these smaller water bodies resulted in significant changes to the network configuration. As expected, when removing these small surface water nodes, the number of edges was reduced and the networks become longer as shown by greater diameter and longer average path length, thus increasing the number of steps an organism would need to traverse the network. The fact that the diameter decreased after a certain percentage of node removal for the highest connected node removal strategy suggests that the networks become disconnected to the degree that the majority of nodes are not part of the core network anymore. Despite the fact that the removal of nodes triggered similar patterns in network topology response for both dry and wet phases, the resulting networks were quite different (figures 3(a) and (b)). The removal of the smallest area nodes and randomly selected nodes disconnected a similar set of nodes. These were the ones located in the Southern part of the network (results not displayed). Conversely, during the wet phase the disconnected nodes were further North, suggesting that the function of the dispersal networks will be highly dependent on whether loss of habitat occurs during a dry or a wet phase as the impact of loss differs between wet and dry phases. The fact that the graph clustering coefficient remained similar for all except the highly connected node removal strategy suggests that the removal of the highly connected water body nodes left a fragmented and sparsely connected network. In dry years the number of water bodies was substantially reduced and they were sparsely distributed and disconnected across the SCP.

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We identified individual ‘stepping-stone’ water bodies that are disproportionally high in importance in preserving the ability of organisms to traverse the fragmented landscape by computing betweenness centrality. Nodes that play a critical role as shortcuts have high betweenness centrality and act as mechanisms to link persistent habitat together and permit the utilization by animals of the landscape despite the high variability in environmental conditions. Here we identified water bodies of high betweenness centrality across seasons and over 13 years including drought and deluge years, and spanning three dispersal distances. The fact that all water
bodies that act as ‘stepping stone’ are located around the Peel-Harvey area suggests the importance of the area to the system connectivity. The Peel-Harvey is a Ramsar listed site for its importance as waterbird area and based on our results we suggest that there are a few water bodies that act as hubs whereas the majority of them have only a few connexions. For the wetlands represented here, the continued protection of the surface water network hubs (e.g., Ramsar sites, natural parks) will likely maintain the landscape health. In particular the prevention of disease spread and invasive species and other disturbances require the networks to be in good health. The types of networks found on the SCP are resistant to random attacks such as random node removal, but not resistant to targeted removals based on connectivity, emphasizing the need to identify and protect the surface water bodies that act as network hubs. This confirms that the topology of the network is important as it affects the resilience of the network when being disturbed.

One caveat should be noted. As with most research investigating spatial networks at landscape scales, the networks presented here are based on the indirect assumption regarding movement rather than observed movement (Fletcher et al 2011). However, this approach represents a cost-effective way of assessing connectivity (Calabrese and Fagan 2004, Urban et al 2009, Fletcher et al 2011) for ecological and conservation biology networks when movement data and cost surfaces are not available. Here we picked three distances that represent different groups of organisms rather than a specific species, but the same analysis can be conducted for a different species of interest especially if actual movement data is collected and cost distances can be incorporated. Fletcher et al (2011) found that compared with social network models, landscape connectivity metrics based on...
maximum distance constructions can overpredict connectivity and provide high estimates of metapopulation lifetime in landscape networks. While the metrics presented in this research represent ‘potential connectivity’, they show in relative terms how the connectivity has changed over time with both intrannual changes in wet and dry years as well as intraannual changes.

Our work has direct implications for conservation planning and represents a way of identifying ‘stepping stone’ water bodies in a biodiversity hotspot that is subject to water abstraction, urban development and climate change. Future work should predict how connectivity may be affected by future climate change with particular emphasis on the alteration of habitat and barriers to dispersal. Climate change and anthropogenic activity (urban development and ground water abstraction) on the SCP will result in decreased availability of surface water, with the expected outcome being a reduction in water levels and size of water bodies as well as losing smaller or temporary surface water bodies (Nielsen and Brock 2009). This can negatively impact the aquatic biota by decreasing available habitat and increasing distance among suitable habitats (Davis and Froend 1999). The network approach utilized to analyse the wetlands in the SCP highlights the functional character of this dynamic yet fragile ecosystem.

Quantifying the spatiotemporal dynamics in network structure of surface water bodies represents a powerful tool for assessing potential survival of species that are dependent on surface water bodies and their regional connectivity. Most studies of this type focused on static landscapes, with few studies including a modelled dynamic (Fortuna et al. 2006). Furthermore, little advancement has been made in quantifying the actual effects of loss of habitats for networks that also undergo natural change across seasons and years (Wright 2010), but this spatial and temporal dynamics of aquatic networks can now be represented as time-series of systematically acquired and characterized remotely sensed data (e.g., Landsat, MODIS).

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