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Surface-water dynamics and land use influence landscape connectivity across a major dryland region

Robbi Bishop-Taylor,[1] Mirela G. Tulbure, and Mark Broich

School of Biological, Earth & Environmental Sciences, University of New South Wales, Sydney, New South Wales 2052 Australia

Abstract. Landscape connectivity is important for the long-term persistence of species inhabiting dryland freshwater ecosystems, with spatiotemporal surface-water dynamics (e.g., flooding) maintaining connectivity by both creating temporary habitats and providing transient opportunities for dispersal. Improving our understanding of how landscape connectivity varies with respect to surface-water dynamics and land use is an important step to maintaining biodiversity in dynamic dryland environments. Using a newly available validated Landsat TM and ETM+ surface-water time series, we modelled landscape connectivity between dynamic surface-water habitats within Australia's 1 million km^2 semiarid Murray Darling Basin across a 25-yr period (1987–2011). We identified key habitats that serve as well-connected "hubs," or "stepping-stones" that allow long-distance movements through surface-water habitat networks. We compared distributions of these habitats for short- and long-distance dispersal species during dry, average, and wet seasons, and across land-use types. The distribution of stepping-stones and hubs varied both spatially and temporally, with temporal changes driven by drought and flooding dynamics. Conservation areas and natural environments contained higher than expected proportions of both stepping-stones and hubs throughout the time series; however, highly modified agricultural landscapes increased in importance during wet seasons. Irrigated landscapes contained particularly high proportions of well-connected hubs for long-distance dispersers, but remained relatively disconnected for less vagile organisms. The habitats identified by our study may serve as ideal high-priority targets for land-use specific management aimed at maintaining or improving dispersal between surface-water habitats, potentially providing benefits to biodiversity beyond the immediate site scale. Our results also highlight the importance of accounting for the influence of spatial and temporal surface-water dynamics when studying landscape connectivity within highly variable dryland environments.

Key words: Australia; flooding; graph theory; land use; Landsat; landscape connectivity; Murray-Darling Basin; protected areas; surface-water dynamics; wetlands.

Introduction

Dryland freshwater environments are among the most vulnerable ecosystems globally (Williams 1999), faced with the combined threats of land-use intensification and changes in water availability driven by increased human consumption and a changing climate (Vörösmarty et al. 2010, Davis et al. 2015). This has resulted in extensive loss (up to 87% by area since 1700 AD) and degradation of biodiverse wetlands due to agricultural and urban development and flow modification (Davidson 2014), isolation of remaining habitats separated by an increasingly modified landscape matrix (Collins et al. 2014), and increasing severity of extreme drought and flooding events (Leblanc et al. 2012). The combined impacts of these changes to surrounding land use and spatiotemporal surface-water dynamics (i.e., drought or flooding) are likely to disproportionately impact the population persistence of dryland freshwater biota by reducing opportunities for dispersal through already variable and fragmented surface-water habitat networks (Ward and Stanford 1995, Davis et al. 2015, Saunders et al. 2015). Maintaining vital landscape-scale processes such as landscape connectivity in ecosystems affected by increasingly intense human use and environmental change remains a key challenge facing conservation in the 21st century (Rudnick et al. 2012).

To mitigate these threats posed to freshwater ecosystems, biodiversity conservation approaches have attempted to preserve ecologically significant surface-water habitats using protected area strategies (Suski and Cooke 2006). Despite being effective at reducing site-scale threats such as conversion of land for agriculture, protected area strategies can fail if they do not address threatening processes operating at landscape, catchment, or basin scales, such as changes to hydrology or reductions in landscape connectivity (Pringle 2001, Berney and Hosking 2016). This may be of particular concern for surface-water ecosystems, given the reliance of water-dependent biota on water availability and variable flooding dynamics for recruitment and dispersal between habitats (Crook et al. 2015). Identifying and managing habitats that preserve or enhance landscape connectivity

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[1]E-mail: r.bishop-taylor@unsw.edu.au

within habitat networks may provide a promising means to maintain population persistence and biological diversity in threatened landscapes (Saunders et al. 2015). These areas could serve as high-priority targets for the provision of limited and contested environmental water, potentially facilitating dispersal and gene flow among isolated surface-water habitats and providing biodiversity benefits that extend beyond protected area boundaries (Arthington 2012, Crook et al. 2015). Prioritizing dynamic surface-water habitats for conservation at a network scale, however, requires a detailed understanding of how spatial and temporal surface-water patterns influence the potential for connectivity, particularly within heterogeneous landscapes affected by varying degrees of modification (Watts et al. 2015).

Graph theory network analysis provides a powerful approach for studying spatiotemporal connectivity patterns. Graph theory allows connectivity to be assessed across large spatial extents by analyzing entire landscapes in a network data structure (Minor and Urban 2007, 2008). For example, individual surface-water habitats in a spatial surface-water habitat network can be depicted as a series of "nodes," with each node representing a potential habitat that can be connected to others by an "edge" (or link) if an ecological connection exists between them (Urban and Keitt 2001). In a spatial habitat network, this may be the case when the distance and landscape conditions between two neighboring habitats allow resident water-dependent species to disperse successfully between them. This spatially explicit analysis framework allows large habitat networks to be compared consistently across both time and space. Graph theory analyses have provided insights into many aspects of connectivity including how the loss or creation of habitats may impact long-distance dispersal and gene flow (Uden et al. 2014), how migrating species may respond to a changing climate (McIntyre et al. 2014, Dilts et al. 2016, McGuire et al. 2016) and how drought or flooding may affect surface-water habitat network structure or metapopulation viability (Fortuna et al. 2006, Wright 2010, Tulbure et al. 2014, Bishop-Taylor et al. 2015).

Algorithms provided by graph theory network analysis can assist in prioritizing conservation management actions by identifying individual habitats that are particularly important for facilitating connectivity within habitat networks. Two of the most important roles a habitat can play are as "stepping-stones" or "hubs" (Ruiz et al. 2014, Saura et al. 2014). Stepping-stones are habitats that allow dispersing organisms or populations to make long-distance movements through networks by providing connections between larger groups of connected habitats. Stepping-stones can be critical for range expansion, particularly as changing climate conditions and habitat loss forces organisms to move long distances through increasingly modified and hostile landscapes (Kramer-Schadt et al. 2011, Saura et al. 2014). Hubs are habitats that are connected to a high number of neighbors relative to other habitats in the network. These habitats provide extensive opportunities for local dispersal, and may serve as important ecological refuges into which organisms can retreat and subsequently disperse from after periods of environmental disturbance (Davis et al. 2013, Bishop-Taylor et al. 2015). Obtaining a better understanding of the importance of individual habitats within habitat networks can therefore assist in maintaining landscape connectivity at scales far beyond immediate sites.

While stepping-stone and hub habitats may represent ideal targets for habitat conservation, their importance is unlikely to be consistent through time (Tulbure et al. 2014). In highly dynamic dryland surface-water environments, only a small proportion of habitats may remain present from year to year or season to season (Roshier et al. 2001). Other temporary or ephemeral habitats may play important roles as connectivity providers only during specific environmental conditions, such as during periods of extreme drought or flood (Zeigler and Fagan 2014). Despite the important implications of spatiotemporal surface-water dynamics for connectivity, previous research has focused on assessing connectivity between static or modelled sets of surface-water habitats (e.g., Fortuna et al. 2006, O'Farrill et al. 2014), or between waterbodies at discrete "snapshots" in time (e.g., Wright 2010, Uden et al. 2014). Little research has quantified how the distribution of important stepping-stones and hubs varies across both space and time in the context of dynamic periods of drought or flooding (Tulbure et al. 2014) or evaluated how these changing distributions interact with current protected area listings or local land-use patterns (Ruiz et al. 2014, Bishop-Taylor et al. 2015).

In this study, we used graph theory network analysis to model spatially explicit patterns of important stepping-stones and hubs using a newly available 25-yr seasonally continuous and statistically validated time series of potential surface-water habitats based on Landsat TM and ETM+ satellite imagery (Tulbure et al. 2016). We focused on assessing connectivity within Australia's Murray-Darling Basin, a major inland river basin containing some of the world's most ecologically significant dryland floodplain and wetland environments (Rogers and Ralph 2010). By conducting, to our knowledge, the largest spatially explicit ecological network analysis to date (a total of 5.4 million nodes processed across 99 time-steps and two dispersal abilities), our study sought to answer the following research questions relating to interactions among landscape connectivity, surface-water dynamics and land-use and conservation management: (1) How does the distribution of important stepping-stones and hubs vary among dry, average, or wet conditions? (2) Are modified land-use types (e.g., grazing or dryland and irrigated agriculture) less likely to contain stepping-stones and hubs than protected or natural areas? (3) How does dispersal ability affect relationships between land use and the distribution of stepping-stones and hubs during dry, average, or wet conditions?

Methods

Study area

We focused on the Murray-Darling Basin (MDB), a 1 million km^2 semiarid basin in southeastern Australia (Fig. 1). Despite being one of the driest catchments in the world by runoff (MDBA 2010), the MDB supports some of Australia's most biologically diverse and ecologically significant floodplain and wetland habitats, including 16 sites listed as Wetlands of International Importance under the Ramsar Convention (Rogers and Ralph 2010, Pittock and Finlayson 2011). Extreme variability in water availability in the MDB drives a characteristic "boom and bust" ecology, with populations of many species fluctuating greatly in response to periods of severe drought and flooding (Ballinger and Mac Nally 2006). Although these extremes are a natural feature of its regional climate, the MDB has recently experienced both the most severe drought and wettest two-year period since instrumental records began: the 1999–2010 Millennium Drought and the 2010–2011 La Niña floods (Mac Nally et al. 2014). These extremes have combined with impacts of wetland loss, water diversions for agriculture, and flow modification to place increasing pressure on surface-water habitats (Finlayson et al. 2011). Reduction in flows to wetlands is believed to be the major factor influencing the ecological health of these ecosystems, with reduced landscape connectivity between habitats a key threat to the persistence of water-dependent organisms (Finlayson et al. 2011).

Seasonal surface water

We studied the connectivity of surface-water habitats across the entire MDB between 1987 and 2011 using seasonally continuous observations of surface-water mapped from Landsat TM and ETM+ satellite imagery (Tulbure et al. 2016). To convert surface-water observations into potential habitat layers, we identified pixels that contained water for greater than 50% of satellite observations within each southern hemisphere season from 1987 to 2011 (i.e., autumn, winter, spring, and summer beginning on 1 March, 1 June, 1 September, and 1 December, respectively). This majority threshold ensured that resulting habitat pixels for each season were typically inundated for approximately 1.5 months, an ecologically relevant value for many aquatic invertebrates (e.g., 1–2 months from eggs to independence for several MDB crustaceans; Jones 2010), amphibians (e.g., 2–4 months tadpole lifespan for the majority of MDB frogs; Wassens 2010) and freshwater turtles (e.g., 60–70 d incubation period near water for common MDB species; Thompson 1983, Kennett and Georges 1990).

We filled areas of "nodata" on a per-pixel basis (Tulbure and Broich 2013) when a pixel was missing data for an entire season (i.e., through consistent cloud cover). "Nodata" pixels were assigned the most common state (surface water or non-water) from the closest three years with data for the respective season, commencing with the previous year (e.g., a nodata pixel in autumn 2007 was filled with values from autumn 2006, 2008, and 2005). To facilitate computationally intensive connectivity analyses for the entire extensive spatial (>1 million km^2) and temporal (99 seasons) data extent, the original 30-m raster pixels were spatially aggregated to 120 m pixels using a maximum aggregation rule that considered aggregated cells as potential habitat if at least one of the 16 contributing pixels contained habitat (McRae et al. 2008). All habitat layer manipulation was conducted using the GDAL (GDAL Development Team 2015), NumPy, and SciPy packages (van der Walt et al. 2011) for Python 2.6 (Python Software Foundation 2015).

Temporally consistent habitat IDs

To consistently compare connectivity across time and space, we assigned each flooded pixel with a unique, temporally consistent, habitat identifier (unique ID). Previous studies have defined discrete, temporally consistent regions based on the maximum extent of flooding across an entire time series to account for surface-water habitats growing, shrinking, or fragmenting over time (Tulbure et al. 2014). In the MDB, however, rare but very large flooding events form extensive "mega-patches" in composite maximum extent data sets that can span hundreds of square kilometers, potentially obscuring ecologically significant seasonal surface-water dynamics. To resolve this "mega-patch problem," we used a simplified version of a method based on habitat asynchrony and graph theory community detection previously used to identify temporally consistent subregions in remotely sensed giant kelp forest time series (Cavanaugh et al. 2014). We initially generated an $m \times n$ matrix of n observations (surface water or non-water for each of the 99 seasons) for each raster pixel m in the study area (Fig. 2A). We converted this matrix into a network graph by connecting surface-water pixels (nodes) to their immediate eight spatial neighbors, and weighted the resulting graph edges by the pairwise Pearson correlation in temporal dynamics between each pixel (i.e., high correlation if the two pixels consistently occurred together as either surface water or non-water throughout the time series; Fig. 2B).

We used the Igraph Python package (Csardi and Nepusz 2006) "community_multilevel" implementation of the Louvain community detection algorithm to divide "mega-patches" into discrete asynchronous potential habitats (Cavanaugh et al. 2014). The Louvain algorithm efficiently partitions large connected graphs into unique "communities" by maximizing the graph's modularity, a measure of the density of within-community links compared to between-community links (Newman 2006, Blondel et al. 2008). As the Louvain algorithm does not accept negative weights, we truncated graph edge weights (correlations ranging from −1 to 1) to between 0 and 1 prior to analysis. The community membership identifiers

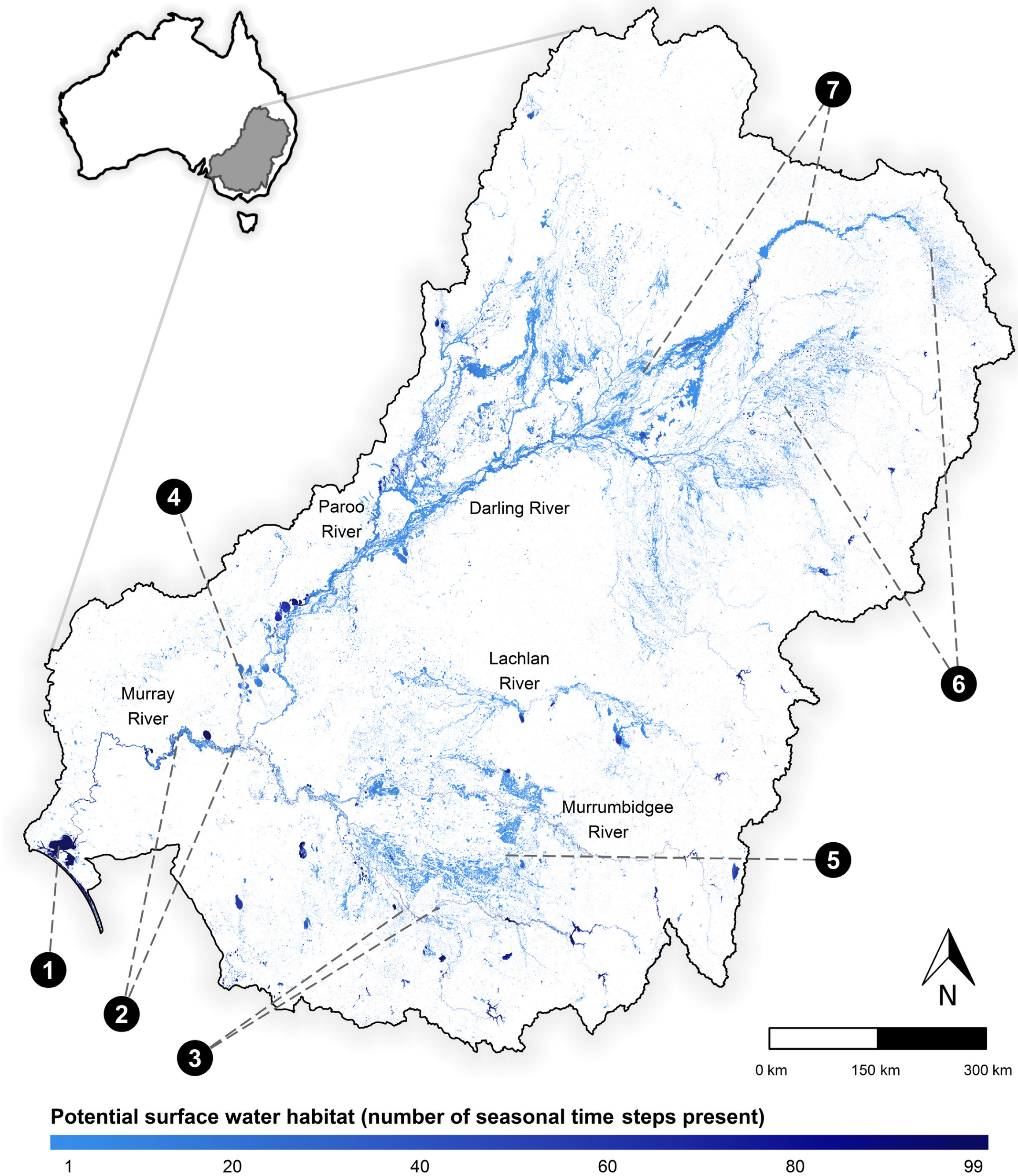

Fig. 1. Murray-Darling Basin (MDB) study area, showing the distribution and frequency of potential surface-water habitats across the entire 99-season time series (dark blue indicates persistent habitats; Tulbure et al. 2016). Numbered annotations highlight significant regions of the MDB discussed in this study: (1) Lower Lakes, Coorong, and Murray Mouth; (2) the River Murray Channel including Riverland Wetland Complex and Lindsay-Wallpolla-Mulcra Islands; (3) Gunbower-Koondrook-Perricoota and Barmah-Millewa Forests; (4) Greater Darling Anabranch; (5) the Riverina agricultural region; (6) irrigated agriculture and floodplains of the Condamine, Gwydir, Namoi, and Border Rivers catchments; and (7) floodplains of the Condamine-Balonne catchment. [Colour figure can be viewed at wileyonlinelibrary.com]

produced by the algorithm were finally converted back into a raster containing 277874 temporally consistent unique IDs informed by both the spatial structure and temporal synchrony of habitats throughout the entire 1987–2011 time series (Fig. 2C). These unique IDs served as individual graph nodes in subsequent network analyses.

To test how successfully each unique ID habitat represented a spatially discrete area of surface water across

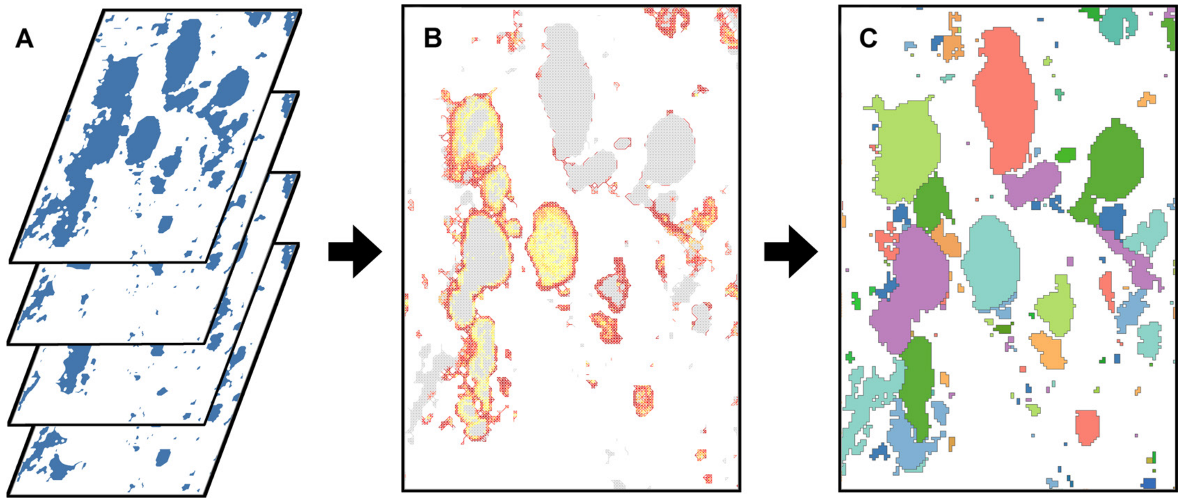

FIG. 2. Example of process followed to break potential habitat areas into discrete "communities" of raster pixels (unique ID regions or graph nodes) that consistently occurred together across time. For all neighboring pairs of pixels within the study area, we assigned weights depending on their asynchrony across the entire 1987–2011 time series (A). These weights (B; yellow to red indicating pixel pairs that rarely occurred together in a single time-step) were then used to identify (C) potential unique ID regions (graph nodes) that typically occurred as discrete areas of habitat except during the largest flooding events. [Colour figure can be viewed at wileyonlinelibrary.com]

each season in the time series, we evaluated the proportion of seasons where surface water was entirely restricted to within each habitat's unique ID boundary (i.e., where no flooding crossed between habitat boundaries). On average, the 277874 habitats identified by the algorithm had no water crossing habitat boundaries for over 90% of seasons, indicating that "mega-patches" were successfully broken into unique regions that remained spatially discrete except during the largest, most infrequent floods.

Circuit theory analysis

We calculated effective distances between unique habitats using circuit theory, a modelling approach based on random walks that takes into account all possible movement pathways through a heterogeneous landscape matrix separating two habitats (McRae et al. 2008). Landscape moisture has been shown to strongly affect movement and connectivity for aquatic invertebrates (Morán-Ordóñez et al. 2015), amphibians (Murphy et al. 2010, Watts et al. 2015), and turtles (Patrick et al. 2012). To account for landscape resistance to movement for a broad range of water-dependent organisms inhabiting the MDB, we used a generalized resistance layer based on landscape moisture (Goldberg and Waits 2010). This resistance layer was generated by classifying Australian Dynamic Land Cover Dataset v1.0 classes (Lymburner et al. 2010) and potentially significant movement barriers or corridors such as roads, streams and urban areas from Geoscience Australia (2006) topographic mapping into six exponentially increasing resistance classes based on assumed ground level moisture content, and combining this with areas that received any inundation during each of the 99 seasons (Table 1).

Pairwise circuit theory resistances (effective distances that account for landscape resistance to movement) between neighboring habitats were calculated for each season using a moving window approach. To allow connectivity between windows and minimize circuit theory edge effects by providing a large buffered area relative to the longest investigated inter-patch distance (Pelletier et al. 2014), we divided the entire study area into 12×12 km "windows" (100×100 raster pixels) that overlapped by 50% (McIntyre and Strauss 2013). Pairwise resistance distances for each window were calculated

TABLE 1. Resistance to movement values used to develop resistance surfaces (based on Geoscience Australia [GA] topographic features and Australian Dynamic Land Cover Dataset [DLCD] v1.0 classes; Geoscience Australia 2006, Lymburner et al. 2010).

Value	Resistance	Example DLCD land cover or GA topographic features
1	very low	surface water (including seasonal maximum flooding extent), aquatic vegetation
2	low	closed natural vegetation, irrigated cropping and pasture
4	moderate	open natural vegetation, dryland pasture
8	moderate-high	sparse natural vegetation, dryland cropping, minor roads
16	high	non-vegetated areas, major roads
32	very high	urban infrastructure and highways, saline waterbodies

using the Circuitscape v4.04 software package (Shah and McRae 2008) with seasonal habitat and resistance layers as inputs (connecting raster pixels to their eight immediate neighbors). When pairs of habitats were analysed multiple times due to overlapping windows, the lowest resistance distance was selected to eliminate artificially high resistance values associated with circuit theory edge effects.

Graph theory network modelling

We generated potential surface-water habitat networks for each of the 99 seasonal time-steps in the 1987–2011 time series using graph theory network modelling, with the matrix of Circuitscape resistance distances between all neighboring habitat pairs as an input. We treated unique habitats as graph nodes, and compared connectivity for two maximum circuit theory resistance distances converted from Euclidean distance values. These resistance distances (0.53 and 1.61) were identified by calculating the 95th percentile of circuit theory movement costs associated with maximum Euclidean dispersal distances of 1000 m and 5000 m (Bishop-Taylor et al. 2015). Distances of 1000 m and 5000 m were selected to encompass the dispersal abilities of a range of common water-dependent organisms within the MDB, including aquatic invertebrates (e.g., 99% of movements below ~1 km for a widespread MDB freshwater crustacean; O'Connor 1986), amphibians (e.g., mean maximum dispersal distance of ~2 km globally; Smith and Green 2005) and freshwater turtles (e.g., dispersal up to ~5 km for a common southeastern Australian freshwater turtle; Roe et al. 2009).

Many studies have highlighted the importance of habitats with high network centrality for maintaining and enhancing landscape connectivity (Urban and Keitt 2001, Estrada and Bodin 2008). We used local graph centrality metrics to evaluate the potential importance of each unique habitat (node) across each of the 99 seasonal time-steps. Degree centrality (DC) measures the numbers of edges (connections) between a node and its immediate neighbors. In a habitat network, habitats with particularly high DC values (e.g., in the top 1% of values) may serve as "hub" habitats whose location and spatial structure provide abundant opportunities for local dispersal (Estrada and Bodin 2008). Betweenness centrality (BC) quantifies the number of times a node occurs on the shortest path between any two nodes in a network, with high values (e.g., top 1%) indicating potential "stepping-stone" habitats vital for enabling long-distance movements. We calculated DC and BC on networks restricted to each of the two dispersal distances using the Igraph Python module (Csardi and Nepusz 2006), with resistance distances as edge weights to ensure shortest paths for BC ran through areas of least resistance to movement.

To identify potential stepping-stones and hubs, we mapped the top 1% of values for each metric and seasonal time-step by ranking habitats from 0 (low importance) to 1 (high importance). This top 1% cutoff was selected to identify a potentially manageable subset of important habitats given the large number of total habitats identified in our study area (i.e., 277874), and to approximate cutoffs used to identify stepping-stones and hubs in previous dynamic connectivity studies (e.g., the top 0.7% or 20 out of a maximum of 2955 wetlands by DC and BC used to identify hubs and stepping stones by Ruiz et al. 2014). Habitats were mapped separately for the driest 25%, average 25–75%, and wettest 25% of seasons by surface water area across the entire MDB to compare how the distribution of top 1% habitats varied spatially and in context of drought and flood. To evaluate whether stepping-stones and hubs were under- or over-represented within various land-use types, we extracted data for seven land-use categories based on the 2010–2011 Catchment Scale Land Use of Australia (CLUM) data set's "Primary" categories (ABARES 2014; Table 2) and identified the majority land-use category for each unique ID habitat using the Extract to Table tool in ArcMap 10.3 (ESRI 2016). Assuming that 1% of habitats within each land-use type would be in the top 1% of habitats by BC and DC basin-wide if these important habitats were randomly distributed with respect to land use, we then calculated the proportion of top 1% basin-wide habitats compared to all habitats within each land use (i.e., a proportion greater than 1% indicated a higher than expected proportion of stepping-stones and hubs within a specific land use, whereas a proportion less than 1% indicated stepping-stones or hubs were underrepresented). This proportion was calculated separately for each seasonal time-step, and plotted by driest to wettest seasons to evaluate how the representation of stepping-stones or

TABLE 2. Land-use categories used to compare distributions of stepping-stones and hubs, based on 2010–2011 Catchment Scale Land Use Map (CLUM) classes (ABARES 2014).

Land-use categoSry	CLUM codes	Example CLUM land uses
Conservation	1.1.1–1.1.7	protected areas
Natural environments	1.2.0–1.3.4, 6.0.0–6.1.3, 6.3.0–6.3.3, 6.5.0–6.6.3	non-protected natural vegetation or surface water
Production from natural environments	2.1.0–2.2.2	grazing on relatively natural vegetation, forestry
Dryland agriculture	3.0.0–3.6.4	dryland cropping, modified pastures
Irrigated agriculture	4.0.0–4.6.3	irrigated cropping and horticulture
Intensive uses	5.0.0–5.9.5	urban areas, mining
Artificial water	6.2.0–6.2.3, 6.4.0–6.4.3	reservoirs, farm dams

hubs per land-use category varied along a spectrum from dry to wet conditions.

Results

Spatial distribution of stepping-stones and hubs

The distribution of important habitats for connectivity varied considerably both between dry, average, and wet seasons and by dispersal ability. During dry seasons, stepping-stones (habitats in the top 1% by BC values) were largely restricted to permanent riverine corridors for both short and long dispersal distances (i.e., ~1000 m and 5000 m, respectively; Fig. 3). These regions included the floodplains of the perennial River Murray and, to a lesser extent, the Murrumbidgee and Darling where persistent waterbodies and wetlands supported long-distance connectivity even during dry conditions. For both dispersal abilities, persistently important stepping-stones occurred along an ~650-km stretch of the Murray between the Ramsar-listed Coorong, Lower Lakes, and Murray Mouth lake and wetland complex (top 1% stepping-stones for up to 94 out of the total 99 seasonal time-steps) to the confluence of the Murray-Murrumbidgee Rivers (up to 97 seasons), and within and upstream of the Barmah-Millewa Ramsar site and wetlands of River Murray Reserve (up to 95 seasons). Although most dry-season stepping-stones for long-distance dispersers followed the main channels of the Murray, Murrumbidgee, and Darling Rivers, other important stepping-stones occurred within the upper reaches of the Gwydir, Namoi, Border Rivers, and Condamine catchments to the northeast of the MDB, and in highly ephemeral surface-water habitat within the Paroo River catchment and the Greater Darling Anabranch (Fig. 3).

During average and wet seasons, top 1% stepping-stone habitats expanded along the Murrumbidgee, Darling, and other smaller ephemeral river systems and agricultural regions in the less modified northern MDB

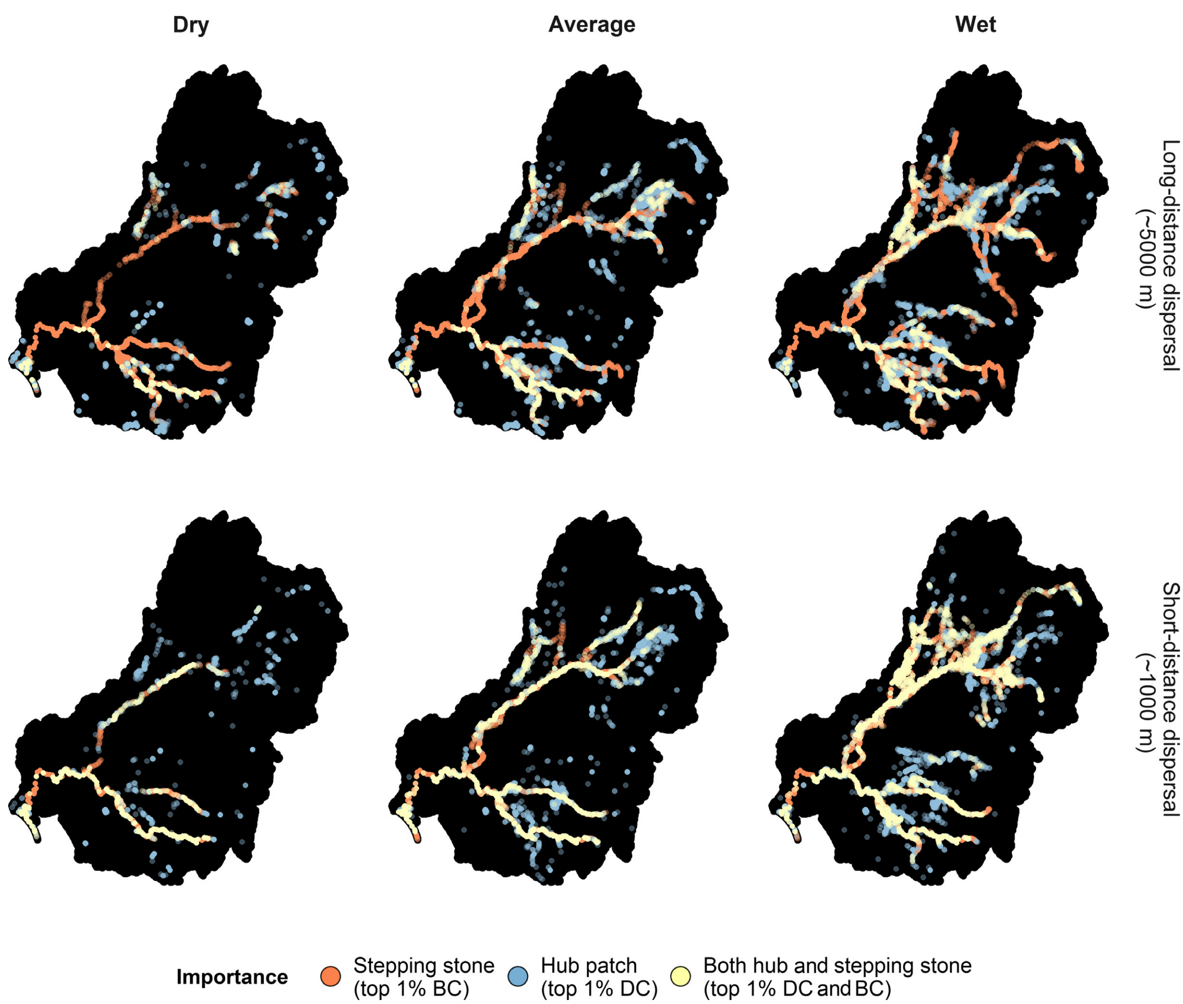

FIG. 3. Distribution of top 1% of stepping-stones and hubs across the MDB. Important habitats are shown separately for two dispersal abilities (short-distance, ~1000 m; long-distance, ~ 5000 m) and the driest 25%, average (25–75%) and the wettest 25% of seasons by inundated habitat area. [Colour figure can be viewed at wileyonlinelibrary.com]

(Fig. 3). Some of the largest increases in stepping-stone prevalence for short-distance dispersing organisms occurred within the highly ephemeral and unregulated Paroo basin. Although a small number of permanent habitats in the Paroo remained connected via stepping-stones for long-distance dispersal organisms during averagely wet periods, these habitats were highly disconnected for short-distance dispersers until large increases in connectivity during wet conditions. Other ephemeral catchments including the Lachlan and Condamine-Balonne also saw large increases in connectivity during only the wettest seasons in the time series for both dispersal distances but more pronounced increases for long-distance dispersal organisms. New stepping-stones during wet periods also occurred away from main river channels within irrigated agricultural regions, such as within the Riverina region where stepping-stones provided shortcuts for movement between the floodplains of the upper Murray and Murrumbidgee Rivers (Fig. 3). These regions typically served as stepping-stones only for long-distance dispersers, with stepping-stones for less vagile organisms being located in closer proximity to river channels.

Hub habitats were less consistent across time and displayed a more dispersed distribution compared to stepping-stones (Fig. 3). During dry seasons, habitats along the Murray and Darling Rivers frequently served as both stepping-stones and hubs, particularly for short-dispersal organisms. These habitats included the nationally significant Riverland Wetland Complex and Wallpolla Island floodplain wetlands along the central Murray (top 1% hubs for 86 and 97 seasons, respectively) and wetlands to the south of the Ramsar-listed Gunbower-Koondrook-Perricoota Forest group (75 seasons). During wet seasons, hubs for long-distance dispersers were more likely to occur across extensive floodplain regions away from the immediate river channel, or within irrigated agricultural regions (e.g., the Lachlan). The prevalence of hubs within irrigated agricultural areas also increased during average or wet conditions, with some of the largest increases occurring in irrigated areas within the Gwydir, Namoi, Border Rivers, and Condamine catchments in the northeastern MDB.

Connectivity in natural and modified landscapes

Conservation and natural environment land uses exhibited significantly higher than expected proportions of stepping-stone habitats for both short- and long-distance dispersal organisms. During dry seasons, conservation areas contained up to 9.5 times more top 1% BC habitats than expected (i.e., 9.5% vs. 1% expected), while natural environments contained up to 7.1 times (Fig. 4). Although these values decreased during increasingly wet seasons, conservation and natural environments retained the highest proportion of stepping-stones of any land-use type across the entire time series. Hub habitats were also consistently overrepresented within conservation areas (up to 7.6 times more than expected), with no clear trend apparent with increasing inundated habitat area aside from a gradual decrease for short-distance dispersal organisms across dry (~3.7%), average (~1.7%), and wet conditions (~1.2%). Although natural environments also saw a steady decrease in the proportion of stepping-stones during increasingly wet seasons, this proportion never dropped significantly below the expected 1% of habitats.

Artificial and modified land-use types typically contained fewer than expected stepping-stone or hub habitats (Fig. 4) despite hosting a far greater proportion of potential surface-water habitat (~87% by area). Several land-use categories consistently showed significantly lower than expected proportions of stepping-stones across the time series. This included dryland agriculture (including cropping and grazing on modified pastures), artificial water (e.g., reservoirs and dams), and intensive land uses (e.g., urban infrastructure and roads), which exhibited extremely small proportions of stepping-stones for short-distance dispersers across dry, average, and wet seasons (~0–0.5% compared to 1% expected). Stepping-stone proportions improved marginally for long-distance dispersers during increasingly wet seasons but remained significantly lower than expected (~0.3–0.6%). Hub habitats were also underrepresented in these land-use types, although with greater differences between dispersal distances (higher representation for long-distance dispersal) and with higher and more variable proportions overall (i.e., typical values between 0% and 0.7% with occasional seasons up to 2%).

The proportions of stepping-stones and hubs within production from natural environments (e.g., forestry and grazing on native vegetation) and irrigated agriculture were higher and showed stronger relationships with inundated area compared to other modified land uses (Fig. 4). Although both land uses showed lower than expected proportions of stepping-stones and hubs during dry seasons, increasingly wet conditions saw both stepping-stone and hub proportions increase to above expected values. Although the increase in stepping-stone and hub proportions for production from natural environments was modest (increases to 1.1–1.4% and 1.1–1.8% for stepping-stones and hubs, respectively), the prevalence of this land use across much of the north and western MDB was sufficient to account for the majority of decreases in proportions observed in other land-use types during wet seasons (e.g., conservation and natural environments). Increases in the importance of irrigated agricultural areas with flooding were far more extreme, with several seasons distributed across the spectrum from average to wet showing extremely high proportions of top hub habitats (up to 10.1% for long-distance and 3.8% for short-distance dispersal). Despite also containing a disproportionately high number of stepping-stone habitats for long-distance dispersal organisms during wet seasons (up to 3%), irrigated agricultural areas contained fewer than expected stepping-stones and hubs for short-distance dispersers across the majority of the time series.

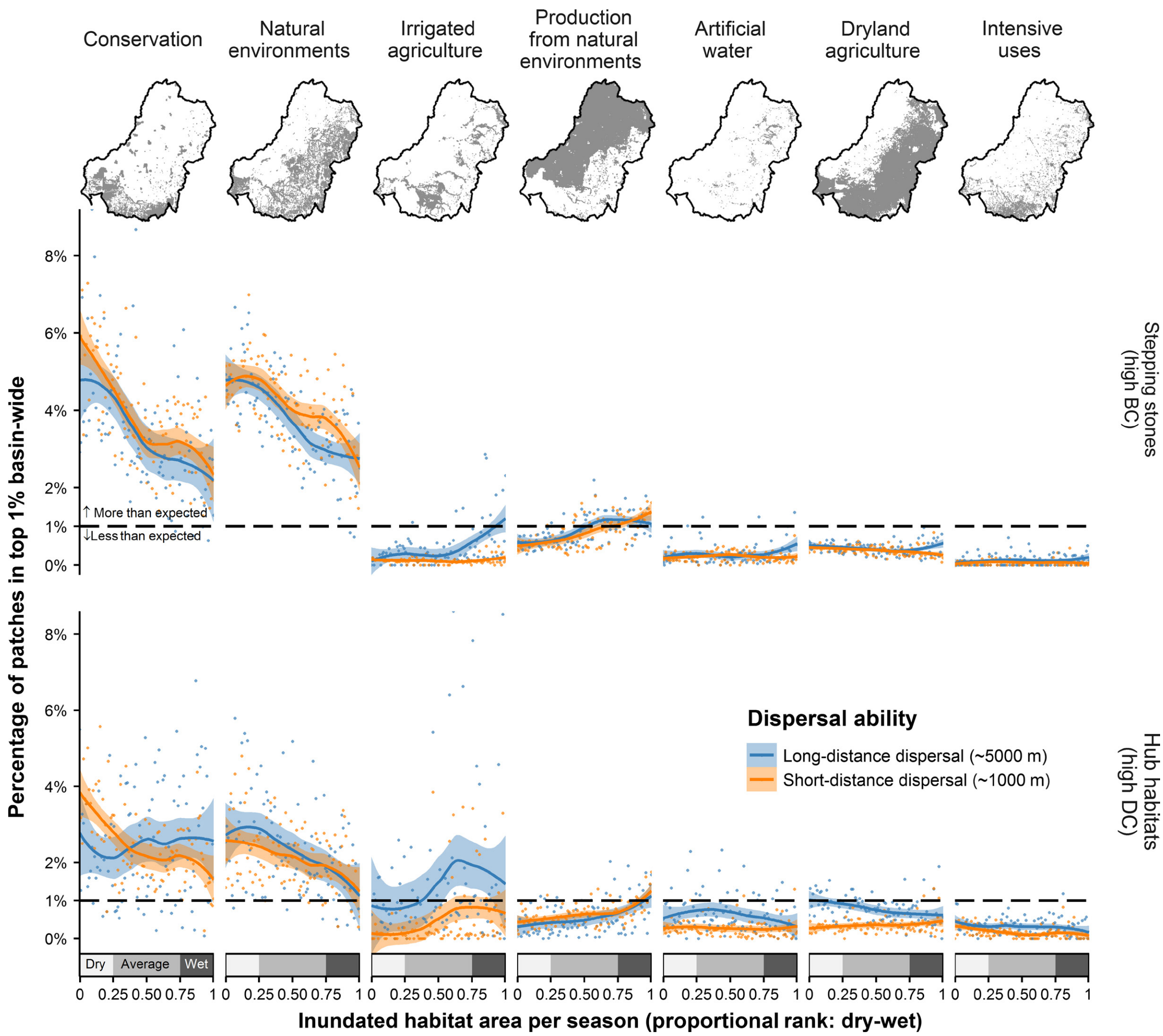

FIG. 4. Top 1% stepping-stones and hubs basin-wide as a percentage of all habitats within each land-use category in the MDB. Percentages are plotted against inundated habitat area (proportional rank) for two dispersal abilities (short-distance in orange, ~1000 m; long-distance in blue, ~ 5000 m), and compared against the expected proportion of 1% (values above 1% indicate more stepping-stones or hubs than expected within a land-use category). [Colour figure can be viewed at wileyonlinelibrary.com]

DISCUSSION

Spatial distribution of stepping-stones and hubs

Landscape connectivity plays a key role in maintaining biodiversity within dynamic dryland freshwater ecosystems (Davis et al. 2015, Murphy et al. 2015). Conservation and management approaches aimed at maximizing connectivity are likely to grow in importance as habitat loss and a changing climate require water-dependent organisms to move long distances in search of suitable habitat or ecological refuges (Nuñez et al. 2013, Davis et al. 2015). However, changing land-use patterns, intensifying water resource demands, and increasingly extreme surface-water dynamics require approaches to maintaining or enhancing connectivity that account for and embrace rapid environmental change and temporal variability (Bond et al. 2008). In this study, we used a comprehensive and spatiotemporally consistent graph theory network analysis approach to model landscape connectivity between potential surface-water habitats within Australia's MDB, a highly modified semiarid region containing some of Australia's most biologically significant wetland ecosystems (Rogers and Ralph 2010, Pittock and Finlayson 2011). We processed over 5.4 million nodes across 99 seasonal time-steps and two dispersal abilities, making our study, to our knowledge, the largest spatially explicit ecological network analyses yet conducted.

We identified a subset of potential habitats that facilitate high levels of connectivity both at local (hubs) and at regional or network scales (stepping-stones). Prioritizing surface-water habitats for conservation based on their potential for improving connectivity through habitat networks may provide an opportunity for maximizing benefits from limited conservation funding and reducing conflict in regions like the MDB faced with changing land-use patterns and increasing demands for water resources. In the MDB, the importance of surface-water habitats as connectivity providers depended on both their spatial position in a habitat network and their persistence and dynamics over time. Large, persistent hub habitats such as those within the Coorong, Lower Lakes, and Murray Mouth lake and wetland complex may serve as important ecological refuges, allowing organisms to survive periods of extreme environmental conditions, including drought. However, landscape connectivity and processes of dispersal into and out of habitats during and after disturbances are critical to refuge function (Chester and Robson 2013). Persistent habitats with highly suitable local-scale habitat attributes (e.g., dense aquatic or riparian vegetation and a lack of predators) may be unable to serve as refuges if they are functionally isolated from other habitats either by geographic distance or by anthropogenic barriers (Sheldon et al. 2010, Davis et al. 2013). Conversely, hub habitats may be less likely to serve as functional refuges if they are present in the landscape for a short period, or if they are highly degraded or otherwise unsuitable for organisms to establish populations or reproduce. Our results therefore do not reduce the importance of collecting site-scale ecological data, but can complement field studies with insights on habitat importance informed by a habitat's context within its larger-scale habitat network.

Stepping-stone habitats that support long-distance dispersal though habitat networks will perform different ecological roles depending on their permanence and relationship with flooding (Bishop-Taylor et al. 2015). Many stepping-stone habitats in the MDB were located within riverine floodplains, where a matrix of permanent and temporary habitats facilitated longitudinal connectivity even during periods of severe drought. By providing connections between clusters of habitats during dry seasons, these stepping-stones may enhance the ability of locally well-connected hubs to serve as functional ecological refuges. This was particularly apparent along the lower Murray River, where perennial stepping-stone habitats provided continuous opportunities for movement between persistent hub habitats within the Lower Lakes and the floodplains of the central Murray. However, other more ephemeral stepping-stones appeared during major flooding across extensive natural floodplains of the northern MDB including within the Condamine-Balonne and Paroo catchments. By creating both new temporary surface-water habitat and stepping-stones connecting existing isolated habitats, transient flooding events in these regions are likely to play a key role in maintaining regional-scale landscape connectivity.

Connectivity in conservation and natural environments

Conservation areas and natural environments in the MDB contained significantly higher than expected proportions of important stepping-stones and hubs throughout almost all seasonal time-steps in our 25-yr time series. Many of these regions contain surface-water habitats already regarded as significant at a national (e.g., Directory of Important Wetlands in Australia) or global (i.e., Ramsar Wetlands of International Importance) scale, of which some have served as previous targets for the allocation of environmental water aimed at maintaining or improving ecological health of habitats stressed by drought. Along the Murray River, several of the stepping-stones and hubs identified by this study (e.g., within the Lower Lakes, Coorong, and Murray Mouth, Gunbower-Koondrook-Perricoota Forests, Lindsay-Wallpolla-Mulcra Islands, and along the River Murray Channel) have been allocated proportions of over 500 GL of environmental water under The Living Murray program, in part to improve connectivity between floodplain and waterways and maintain ecological refuges during the worst of the 1999–2010 Millennium Drought (MDBC 2005). The provision of strategic environmental flows to high-priority stepping-stone and hub habitats will be important to maintain ecological connections between both local and distant clusters of habitats, and may assist in greatly reducing the adverse impacts of severe drought on water-dependent species (Arthington 2012).

The high importance of conservation and natural environments corroborates previous static connectivity modelling in the Murray-Darling that found individual habitats located within protected areas displayed higher BC and DC values than unprotected habitats, especially during large modelled flooding scenarios (Bishop-Taylor et al. 2015). However, our dynamic study showed that while individual habitats within conservation areas may be important for maintaining connectivity during flooding, they represent an increasingly small proportion of total stepping-stones and hubs across the entire MDB during wet seasons. This is likely to reflect two major underlying processes: a basin-wide shift in important habitats towards the less-modified northern MDB during wet periods, and a local shift away from immediate river channels and into more extensive floodplain environments. Conservation areas cover a relatively small proportion of the MDB (~7.5% by area), with protected rivers and wetlands exhibiting a strong bias towards the southern MDB (Bino et al. 2016). Although this spatial distribution provides disproportionally high protection to persistent stepping-stones and hubs located along the floodplains of the Murray River, conservation areas provide less protection for more transiently important habitats that appear across the northern MDB during major inundation events.

Increasing the regional- or continental-scale effectiveness of the Australian protected area network for preserving freshwater biodiversity is likely to require an increase in the representation of stepping-stones and hubs that are important for facilitating landscape connectivity across the northern MDB. Many of these surface-water habitats are located in relatively natural environments used predominantly for grazing and other forms of low intensity production, and so may still provide local-scale habitat attributes required to support populations of water-dependent species, provided they are protected from future land-use intensification (Chester and Robson 2013). Where protected area listings are not compatible with increasingly intensive land uses, increased management may be required to ensure that potential stepping-stones and hubs can support long-distance movement through ecological networks, or serve as ecologically functional refuges. A range of management techniques have shown promise in improving the suitability of artificial surface water to serve as ecological refuges or stepping-stones. These include promoting riparian and aquatic plant growth by reducing the steepness of dam or canal edges (e.g., Robson and Clay 2005, Hamer et al. 2012), fencing to minimize livestock erosion (e.g., Markwell and Fellows 2008, Canals et al. 2011) and attempts to reduce predation by removing introduced fish species (e.g., Vredenburg 2004). The stepping-stones and hubs identified by this study may provide priority targets for management, allowing limited conservation funding to be allocated to habitats that serve as the most effective connectivity providers.

Connectivity in modified environments

Surface water within irrigated agricultural areas in the MDB served as important stepping-stones and hubs during average and wet seasons, but predominantly for organisms with long-distance dispersal abilities. These landscapes were typically characterized by a shifting mosaic of uniformly distributed, temporarily flooded fields and irrigation canals. Although this habitat structure did not prevent inter-patch movement for long-distance dispersers, irrigated agricultural habitats remained disconnected for short-distance dispersal organisms less able to move between the spatially dispersed areas of surface water present at any moment in time. Other less transient artificial water sources (i.e., farm dams and reservoirs) also displayed significantly lower than expected connectivity across the majority of the time series, particularly for short dispersal distances (Fig. 4). A similar result was observed by Uden et al. (2014) in a graph theory study of amphibian habitat networks in the Rainwater Basin (central United States), where smaller, shorter-distance dispersers displayed sharply reduced connectivity in agricultural landscapes dominated by uniformly distributed irrigation water storage pits.

These findings suggest that the regular, dispersed spatial structure of surface-water habitats in highly modified agricultural landscapes disproportionately affect connectivity for short-distance dispersers compared to the tightly clustered matrix of ephemeral and permanent floodplain and wetland habitats they have replaced. Although organisms with long-distance dispersal abilities (i.e., dispersal distances of ~5000 m and above) may be able to successfully move through these landscapes, less vagile organisms may suffer increased genetic isolation and heightened risks of local extinction events due to reduced opportunities for dispersal (Johst et al. 2002). Hydrologic management practices (i.e., maintaining a subset of flooded fields during fallow phases) aimed at mimicking natural mosaics of temporary and permanent habitats have shown success in maximizing aquatic macroinvertebrate biodiversity (e.g., Stenert et al. 2009), and may be required to enhance the persistence of short-distance dispersal species in these modified landscapes. In addition to enhancing connectivity, managing artificial surface-water hydroperiods may also provide ecological benefits at site scales, including ensuring that during even dry periods aquatic organisms such as amphibians or invertebrates have continuous access to relatively persistent surface water in which to complete larval or juvenile stages of their lifecycles (Wassens et al. 2008, Canals et al. 2011).

Limitations and future work

By allowing us to model spatiotemporal connectivity dynamics consistently across space and over a ~25-yr period, our application of remotely sensed surface-water data sets advances previous graph theory network analyses that relied on modelled flooding scenarios (e.g., Bishop-Taylor et al. 2015) or historical and hypothetical future wetland maps (e.g., Uden et al. 2014). Nevertheless, some important caveats in our approach should be noted. As our work was based on remote sensing data sets, our findings are conditional on both the accuracy and availability of input data. This is particularly significant for graph theory network analyses that can be highly sensitive to variation in the number and distribution of nodes (i.e., habitats) used to model connectivity (Butts 2009). The surface-water time series we used to define potential habitats through time was subject to a statistically rigorous accuracy assessment (Tulbure et al. 2016), with a high resulting accuracy for surface water during both wet and dry years (producer's accuracy of 87% ± 3% [mean ± SE]). In addition, temporally aggregating surface water by ensuring that a cell was flooded for at least 50% of each seasonal time-step is likely to have significantly reduced errors of commission by eliminating noisy pixels that may have only occurred once throughout the entire time series.

Where minimal satellite coverage or extended presence of clouds resulted in areas with no data that persisted throughout an entire season, we used a conservative gap-filling method in which cells were filled based on the nearest seasons with data. As reported by Tulbure et al. (2016), large areas of no data in the MDB surface-water time series were concentrated in a minority of (mostly winter) seasons towards both ends of the time series, minimizing their influence on the analysis. The resulting surface-water layers are expected to be far more accurate than previous static layers used to model connectivity in the MDB, such as the Geoscience Australia (GA 2006) topographic waterbody features used by Bishop-Taylor et al. (2015), which have coarse resolution (1:250000), a highly variable provenance (1965–2004 in a single static data set) and inconsistent attribution (Bino et al. 2016). Our use of freely available satellite data with global coverage (i.e., Landsat TM and ETM+) also ensures our approach is generalizable to other regions, allowing our findings to be compared and assessed consistently against other dynamic surface-water environments.

To focus on identifying habitats whose location within surface-water habitat networks was important for facilitating landscape connectivity, we limited this study to using centrality metrics (DC and BC) that quantified only network topology or structure. However, our flexible graph theory framework supports future approaches that could make use of advanced metrics that additionally incorporate habitat quantity, quality, or the relative probabilities of movement between two habitats. In particular, metrics based on the concept of habitat availability or reachability including the Integral Index of Connectivity and Probability of Connectivity have been empirically shown to provide information on the importance of habitats for connectivity that complements and improves upon centrality methods (Saura and Pascual-Hortal 2007, Saura et al. 2011). Combining dynamic surface-water data with these advanced methods would allow interactions between flooded area and regional-scale connectivity to be compared holistically across time and space, potentially providing valuable insights into the structure and resilience of natural and artificial surface-water habitat networks during periods of extreme hydroclimatic variability.

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Data Availability

Data associated with this paper have been deposited in the Dryad digital repository https://doi.org/10.5061/dryad.qf83q