AN ADAPTIVE CYCLE HYPOTHESIS OF SEMI-ARID FLOODPLAIN VEGETATION PRODUCTIVITY IN DRY AND WET RESOURCE STATES

Rajesh Thapa*, Martin Thoms and Melissa Parsons

Riverine Landscapes Research Laboratory

Geography and Planning

University of New England

NSW 2351

Australia

*Author for correspondence

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1002/eco.1609

ABSTRACT

Spatial and temporal variability in flooding plays a significant role in the productivity of semi-arid floodplain ecosystems. Floodplains may be perceived as boom-bust systems but this model does not account for transitions that may occur between wet and dry floodplain states. This study used the concept of adaptive cycles to examine how floodplain vegetation productivity changes in response to wetting and drying. Floodplain vegetation productivity was tracked through a wet and dry state using the Normalized Difference Vegetation Index (NDVI). Floodplain inundation revealed complex vegetation productivity responses to resource availability. There was low NDVI in the dry phase, whereas vegetation vigour increased and decreased through the wetting, wet and drying phases. There was a marked difference in NDVI class area, number of transitions, direction of transitions, probability of transitions and NDVI class diversity between the dry phase and the combined wetting, wet and drying phases of floodplain inundation. The distribution of transition probabilities was platykurtic in dry phase and bimodal during the wetting, wet and drying phases. Overall anti-clockwise hysteresis was the dominant direction of hysteresis. All vegetation productivity measures demonstrated a switch in direction during the wet phase. This hysteresis observed in this study indicates the cyclic nature of vegetation response to floodplain inundation through dry, wetting, wet and drying phases. We propose that vegetation productivity response follows an adaptive cycle and that this is an appropriate model for understanding the complexity of semi-arid floodplain vegetation response to wetting and drying.

Keywords: Resilience, complex response, floodplain ecosystems, Adaptive cycle, NDVI

INTRODUCTION

Semi-arid floodplains are characterized by variable productivity, driven by spatial and temporal variability in flood inundation (Walker *et al.*, 1995; Bunn *et al.*, 2006). During extended periods of limited water availability that may last for years, floodplain primary and secondary productivity is relatively low (Arthington *et al.*, 2010; Parsons and Thoms, 2013). In contrast, flooding stimulates a rapid increase in floodplain productivity that may be maintained for months (Thoms, 2003; Bunn *et al.*, 2006; Leigh *et al.*, 2010). Flooding stimulates water bird migration and breeding (Kingsford *et al.*, 1999; Roshier *et al.*, 2002), fish breeding (Puckridge *et al.*, 2000; Balcombe *et al.*, 2007; Balcombe and Arthington, 2009), increases vegetation productivity (Sims and Thoms, 2002; Capon, 2003; Westbrooke *et al.*, 2005; Reid *et al.*, 2011) and the availability of soil nutrients (Baldwin and Mitchell, 2000; Thoms, 2003; Baldwin *et al.*, 2013a). Semi-arid floodplain ecosystems are therefore perceived to change between two states: a dry 'bust' state of limited water availability and a wet 'boom' state of abundant water availability and productivity (Walker *et al.*, 1995).

Ecosystems respond in a complex manner to the availability of resources (Schwinning and Sala, 2004; Smith *et al.*, 2009) and may show multiple stable states, non-linearity and self-organization (Holling, 1973; Holling and Gunderson, 2002; Folke *et al.*, 2010). Emphasis on floodplain productivity as consisting of two states may not account for the potential complexity in response to water availability. Examining semi-arid floodplains through an adaptive cycle lens may help to better understand the complexity of floodplain productivity response to the intermittent availability of water. Derived from complex adaptive systems theory, the concept of adaptive cycles provides a framework to understand the dynamics of change in complex systems (Holling and Gunderson, 2002). Adaptive cycles describe change as a cyclic process with four phases: exploitation, conservation, release and reorganization

(Holling and Gunderson, 2002). In the exploitation phase, the system is engaged in rapid growth to exploit available resources (Walker and Salt, 2006). Through the conservation phase, biomass gradually builds with energy and materials accumulating in the system. The release phase is triggered by an internal or external disturbance. In the release phase the biomass, energy and materials stored in the system are released, providing a template for the reorganization phase. In the reorganization phase the ecosystem reorganizes into the same state or into a new configuration via an exit cycle (Walker and Salt, 2012). The cyclic movement of an ecosystem through the adaptive loop is linked to resilience, where a resilient system has the structural and functional diversity to move through cycles of release and reorganization without transforming to an alternative state (Holling and Gunderson, 2002). Despite the potential for adaptive cycles to decipher complexity in the response of floodplain ecosystems to water availability, there has been limited application of this concept in floodplains (but see Colloff and Baldwin (2010) and Whalley *et al*. (2011) for exceptions). The aim of this study is to examine how semi-arid floodplain vegetation productivity changes in response to floodplain inundation and drying, and to evaluate whether observed responses correspond to an adaptive cycle.

STUDY AREA

The Narran floodplain is a terminal floodplain wetland complex in the Condamine-Balonne River catchment, Australia (Figure 1). The Narran floodplain covers 296 km² (29,600 ha) and is geomorphologically complex, with numerous lakes, channel networks and dissected floodplain surfaces (Figure 1). The climate of the Narran floodplain is semi-arid with average maximum summer and winter temperatures of 36° C and 19° C respectively. Mean annual rainfall is 448 mm at Collarenebri (1940 – 2009) while mean annual evaporation is 2,250 mm y^{-1}. Rainfall is highly variable with annual rainfall ranging from 144 mm (2002) to 957 mm

(1950). Most rainfall in the Condamine-Balonne River catchment occurs in the well-watered uplands in the summer months (November – February) associated with tropical monsoonal activity.

Water is delivered to the Narran floodplain along the Narran River (Figure 1). The long term mean annual discharge (1965 – 2009) of the Narran River at Wilby Wilby, just upstream of the Narran floodplain is 128,717 ML with a range of 690,000 ML to 1003 ML. There are periodic dry and wet resource states in the Narran floodplain arising from this flow variability in Narran River hydrology (Murray *et al.*, 2006). Flows in excess of 13,000 Megalitres per day (MLD) in the Narran River at the Wilby Wilby gauge result in the initial wetting of the northern floodplain surface. The Northern floodplain fills in sequence through Clear Lake, Back Lake and Long Arm (Figure 1). Water continues along the main Narran River or flows overland to Narran Lake (Figure 1), which can retain water for around 12-15 months. The Narran floodplain remains dry approximately 60% of the time (Rayburg and Thoms, 2009). However, the drying and wetting of the Narran floodplain has been severely impacted by water resource development in the upper catchment. Water extraction has reduced the median annual flow in the Narran River by approximately 30% (Rayburg *et al.*, 2006), significantly reducing moderate-sized floods to the Narran floodplain (Thoms *et al.*, 2007).

The Narran floodplain was gazetted as a National Park in 1988 and listed as a Ramsar wetland of international importance in 1999. Floodplain vegetation cover is dominated by the perennial shrub lignum (*Duma florulenta*). There is an overstorey of riparian woodland along main watercourses including river red gum (*Eucalyptus camaldulensis*), coolibah (*Eucalyptus coolabah*) and black box (*Eucalyptus largiflorens*). A range of woodland communities found in the Narran floodplain includes poplar box (*Eucalyptus populnea*), whitewood (*Atalaya hemiglauca*), belah (*Casuarina cristata*), gidgee (*Acacia calcicola*), wilga (*Geijera* *parviflora*), black box (*Eucalyptus largiflorens*) and whitewood (*Atalaya hemiglauca*). Lignum shrubland and tree communities cover approximately 151 km^2 (51 %) of the Narran floodplain. Grassland covers approximately 42 km^2 (14 %) and consists of Mitchell grass (*Astrebla* spp.*)*, neverfail (*Eragrostis setifolia*) and box grass (*Paspalidium constrictum*) interspersed among clumps of trees and shrubs. There is minor crop and pasture cover (48 km^2 - 16%) and the remaining areas are lakes and barren ground cover (55 km^2 - 19%).

METHODS

Satellite image selection

We used remotely sensed satellite images to track the productivity of vegetation through a dry resource state (DRS) and a wet resource state (WRS) within the Narran floodplain. A three-step process was used to obtain satellite images for analysis of vegetation productivity. First, DRS and WRS were defined. A DRS is a period of no flow or flow below the long-term 95-percentile flow, combined with below average rainfall. In a DRS, there is no moisture subsidy to the floodplain through flooding or rainfall. There is no groundwater influence as regional groundwater levels are more than 100 m below the floodplain surface (Fitzpatrick *et al.*, 2005). A WRS was defined as flow periods above 13,000 MLD in the Narran River at Wilby Wilby; that flow required to initiate floodplain inundation (Rayburg and Thoms, 2009).

Second, we searched flow and rainfall records for conditions matching our definition of dry and wet resource states. Daily Narran River flow data (January 1980 – December 2009) were acquired at Wilby Wilby gauge. Daily rainfall data for the same period were obtained for the area. Monthly discharge and rainfall means were calculated and each month in the record was then delineated as being above or below average or as having no flow or rainfall. Periods fitting the DRS and WRS definitions were then identified in the flow and rainfall record.

Third, we examined the availability of monthly Landsat imagery corresponding to the DRS and WRS periods using the Geoscience Australia ACRES and USGS catalogues. The Narran floodplain is encompassed in one Landsat scene (Path 92, Row 81). Care was taken to select high quality images with no or minimum cloud cover. From the pool of high-quality satellite images we randomly selected 2002 as the DRS and 2004 as the WRS. A total of 23 images, at approximately monthly intervals were selected for this study.

The WRS images were also processed in ERDAS imagine software to delineate the expansion and contraction of floodwaters across the floodplain. To map the extent of inundation, pixels representing water and non-water were identified by performing density slicing, which used threshold reflectance values recommended by Overton (2005). In a number of images the detection of inundated pixels was not possible using a single band because of the presence of a dense vegetation canopy. For those images we used the moisture related index (Normalised Difference Water Index) of Xu (2006) and an unsupervised classification method to differentiate the inundated and non-inundated pixels. Both methods have been successfully used to map inundation across Australian floodplains using Landsat satellite imagery (cf. Frazier and Page 2000; Shaikh *et al*., 2001; Rayburg and Thoms 2009; Thomas *et al*., 2010). The results from both methods were then combined to map the expansion and contraction of floodwater across the Narran floodplain and to calculate the area of inundation in each image.

Calculation of NDVI

Vegetation productivity was tracked through the DRS and WRS at approximately monthly intervals for approximately one year (Table 1). Images were re-sampled to 25 metre resolution and re-projected to the Geodetic Datum of Australia 1994 Universal Transverse Mercator zone 55S, to ensure images from different sources (i.e. from the Geoscience

Australia and USGS catalogues) were of the same resolution. The aligned image digital numbers were converted to top of atmosphere reflectance using the methods of Chander *et al.* (2009). A relative radiometric normalisation was performed using dark and light targets to make images acquired on different dates comparable (Myeong *et al.*, 2006). The Normalized Difference Vegetation Index (NDVI) was calculated in each image as NDVI = $\rho nir - \rho red / \rho nir + \rho red$, where ρ is the spectral reflectance values of spectral bands nir (band 4) and red (band 3) of Landsat TM/ETM+ Images. The NDVI measures vegetation greenness and is a surrogate for vegetation productivity (Lillesand and Kiefer, 2000; Farina, 2006; Wen *et al.*, 2012). Entropy analysis, a non-parametric clustering technique, was performed on the 473,142 NDVI pixel values to determine the minimum number of NDVI groups accounting for the greatest variance in the data set. In addition, a moving window analysis was undertaken to identify breaks in the distribution of NDVI values, following the methods of Parsons and Thoms (2013). Six NDVI classes emerged from the range of NDVI values of < 0 to 0.792. Group 1 is no greenness (NDVI <0). Group 2 (NDVI 0-0.072), Group 3 (NDVI 0.072 – 0.207), Group 4 (NDVI 0.207-0.459), Group 5 NDVI (0.459-0.666) and Group 6 (NDVI > 0.666) represent a continuum of increasing vegetation greenness.

Analysis of vegetation productivity

The area of floodplain in each NDVI class was calculated for each image in the DRS and WRS. NDVI Class 1 was excluded because this area has no greenness and corresponds to water bodies and bare land. To examine change in productivity, pair-wise transitions between NDVI classes in sequential monthly images were calculated on a pixel-by-pixel basis. Each pixel was classified into a change class (C_{ij}) which represents a change from NDVI class *i* to NDVI class *j*. A total of 36 C_{ij} were possible among the six NDVI classes, including six constant classes, and 30 directional change classes. The total area of floodplain that increased or decreased in NDVI class between sequential images (termed a period) was calculated. First-order Markovian transition models (Weng, 2002; Bolliger *et al.*, 2007) were used to model the area, number, direction and probability of change of NDVI classes between sequential images. The Markovian transition model consists of the area of each NDVI change class (C_{ij}) present in each period and the probability (P_{ij}) of each C_{ij} occurring. The number of transitions and the direction (single or two-way) of transitions between NDVI classes were tallied from a pictorial representation of the Markovian transition model. Probability of change (P_{ij}) was calculated as the proportion of the total area of NDVI class i that transitioned to NDVI class j.

The diversity of NDVI classes in each image was calculated using the Shannon-Wiener diversity index, as recommended by Magurran (1988) for large and continuous datasets. In calculating diversity, monthly images are considered as samples, NDVI classes as species, and NDVI area as abundance.

Change in vegetation productivity over time was examined in relation to floodplain inundation. Vegetation productivity measures from each image (NDVI class area, number of transitions, direction of transitions, probability of transitions and diversity of NDVI class area) were plotted against the corresponding area of floodplain inundation in order to explore the existence of hysteresis loops. The direction of the loop, location of change in loop direction and steepness of the loop were assessed from each plot. Hysteresis-driven systems will have multiple transitions over time, a bimodal distribution, and change in a loop pattern in response to driving parameters (Schroder *et al.*, 2005).

RESULTS

Floodplain inundation in the DRS and WRS

The availability of water as a resource differed markedly between the dry and wet floodplain states. Surface water was not visible on the floodplain during the DRS (Figure 2). Flow in the Narran River resulted in floodplain inundation of up to 35 km^2 during the WRS and corresponded to a pattern of expansion and contraction of floodwater (Figure 2). The initial rapid expansion of floodwaters across the floodplain (images 13 to 14) was followed by a phase of high floodplain inundation (images 15 to 18) (Figure 2). The phase between image 19 and 20 was associated with an initial rapid contraction of floodwaters and decrease in area of inundation, followed by gradual contraction of floodwater through images 20 to 23 (Figure 2). Thus, the WRS is not uniform but is made up of three distinct phases of inundation: wetting, wet and drying (Figure 2). The DRS is uniform and comprises a dry phase only. From here forward we report aspects of floodplain vegetation productivity in relation to these four phases.

Vegetation productivity

The area of floodplain associated with vegetation vigour (i.e. NDVI Classes 2-6) was greater during the dry phase (mean area of NDVI Classes 2-6 across the dry phase = 98 km^2; range = 0.71 km^2 - 285 km^2) than the wetting, wet and drying phases combined (mean of NDVI Classes 2-6 across the wetting, wet and drying phases = 55 km^2; range = 0.004 km^2 - 171 km^2). However, the quality of vegetation vigour differed between phases. In the dry phase, NDVI Class 3 was consistently dominant in area (Figure 3). NDVI Classes 2, 3 and 4 were also present during the dry phase (Figure 3). In the wetting, wet and drying phases the dominant NDVI class was not consistent (Figure 3). In the first image of the wetting phase NDVI Class 2 was dominant but NDVI Class 3 was dominant in the remainder of the wetting phase (Figure 3). NDVI Classes 2, 3, 4 and 5 were present during the wetting phase (Figure 3). In first two images of the wet phase NDVI Class 3 was dominant but NDVI Class 4 dominated the third image and NDVI Class 3 dominated the fourth image (Figure 3). All NDVI classes were present during the wet phase (Figure 3). In the drying phase, images 19 and 20 were dominated by NDVI Class 3, then by NDVI Class 2 through the remainder of the drying phase (Figure 3). NDVI Classes 2, 3, 4 and 5 were present during the entire drying phase (Figure 3). Thus, the area of floodplain with vegetation vigour was higher in the dry phase than in the wetting, wet and drying phases. However, vegetation vigour was of higher quality in the wetting, wet and drying phases, with very high vegetation vigour (NDVI Class 6) only present during the wet phase.

Vegetation productivity change

The area and broad direction of change (increase or decrease) between the six NDVI classes differed between the flood and dry phases. The area of floodplain that changed NDVI class between consecutive monthly images (henceforth called a period) was greater in the wetting, wet and drying phases than the dry phase (Figure 4). However, in all phases the area of change is made up of increases and decreases in NDVI class, indicating variability in vegetation productivity. In the wetting phase, an average 143 km^2 of floodplain area changed NDVI class each month and most of this change (82%) came from increasing NDVI class (Figure 4). In the wet phase, an average 151 km^2 changed NDVI class and most of this change (63%) came from increasing NDVI class (Figure 4). In the drying phase, an average 131 km^2 changed NDVI class and most of this change (74%) came from decreasing NDVI class (Figure 4). This contrasts with the dry phase, where an average of 53 km^2 changed NDVI class each month, about half (54%) of which was from decreasing NDVI class and about half (46%) from increasing NDVI class. However, the marked increase and decrease in NDVI during periods 4 and 5 is an apparent anomaly, associated with a small pulse of water along the Narran River (Table 1).

The Markovian transition models demonstrate marked complexity in the area, number, direction and probability of transitions between NDVI classes in the flood and dry phases. The area of an NDVI class was more stable in the dry phase than the wetting, wet and drying phases (Figure 5). Across all periods of the dry phase an average 242 km^2 of the 296 km^2 floodplain area was concentrated in NDVI Class 3 (Figure 5a). In contrast, in the wetting, wet and drying phases floodplain area was spread across all NDVI classes (Figure 5b). The number of transitions among NDVI classes differed markedly among the flood and dry phases. Overall, there were 81 transitions among NDVI classes in the dry phase (average: 7 transitions, range: 4 to 11 transitions; Figure 5a) and 225 transitions in the wetting, wet and drying phases combined (average: 22 transitions, range 16 to 27 transitions; Figure 5b), indicating that change among NDVI classes is greater when the floodplain is wet than when it is dry. Within a flood, the greatest number of transitions occurred in the wet phase (average: 25 transitions range 24 to 27 transitions; Figure 5b). The drying phase had a moderate number of transitions (average: 22 transitions, range 16 to 28 transitions; Figure 5b), and the wetting phase had a lower number of transitions (average: 19 transitions, range 16 to 21 transitions; Figure 5b). Of the 30 possible directional transitions 11 transitions occurred in the dry phase, 21 in the wetting phase, 28 in the wet phase and 23 in the drying phase. The wet phase had the most transitions, with 28 of the 30 directional transitions occurring during maximum inundation.

The direction of transitions between NDVI classes also differed among the four phases. Single and multi-direction transitions between the NDVI classes occurred in all phases, but the ratio of single to two-way transitions was higher in the dry phase than the wetting, wet and drying phases combined. The average ratio of single to two-way transitions was 1.25 in the dry phase compared to 0.33 for the wetting, wet and drying phases combined. Thus, the dry phase is dominated by single direction transitions among NDVI classes while the wetting, wet and drying phases are dominated by two-way transitions. In the dry phase, single direction transitions were largely to or from NDVI Classes 1, 2 and 3 (Figure 5a). In the wetting, wet and drying phases, transitions were two-way among all NDVI classes (Figure 5b). For example in period 18 of the wet phase, there were four or more changes from or to each NDVI class (Figure 5b).

The probability of transitions between NDVI classes also differed between the dry and flood phases. The distribution of transition probabilities in the dry phase was platykurtic (Figure 6). Change between NDVI classes was dominated by low (< 1 %) and high (>50 %) probability transitions (Figure 5a and Figure 6). In the combined wetting, wet and drying phases the distribution of transition probabilities was bimodal (Figure 6). There was a dominant peak at the <1 % probability class (Figure 5b and Figure 6) indicating that most of the transitions that occurred between NDVI classes in the wetting, wet and drying phases were low probability transitions. However, transitions were spread across all probabilities and a secondary peak occurred in the 20-50 % probability class (Figure 6).

Diversity of vegetation productivity

The diversity of NDVI class area was generally higher in the wetting, wet and drying phases than the dry phase (Figure 7). The dynamism of transitions is expressed in the behavior of the Shannon-Wiener diversity index during each phase. In the dry phase, diversity was relatively stable (mean: 0.56; range 0.51-0.69) until image 7 when diversity declined markedly, reaching a minimum of 0.2 in image 11 (Figure 7). In contrast, diversity increased during the wetting phase, varied between 0.98 and 1.40 in the wet phase and then dropped slightly to average 1.16 through the drying phase (Figure 7).

Cyclic change of vegetation productivity in relation to floodplain inundation

A distinct loop is evident in all vegetation productivity measures in relation to the surface area of floodplain inundation (Figure 8; Table 2). Overall, anti-clockwise hysteresis was the dominant form of hysteresis, although several vegetation productivity measures (change in NDVI Class 2, single direction transitions, probability of transition 1-5 % and diversity) demonstrated clockwise hysteresis (Table 2). All vegetation productivity measures demonstrated a switch in direction during the wet phase: a switch of direction was not observed in any other phase (Table 2). The switch during the wet phase was flat for most vegetation productivity measures, but the higher NDVI classes (Class 4, 5 and 6), single direction of change and low probability of transition (<1%) had a steep switch (Table 2). This indicates that measures of vegetation productivity decline or increase sharply during the wet phase, corresponding to a switch of direction in the hysteretic loop.

DISCUSSION

Vegetation productivity responses to wetting and drying

Colloff and Baldwin (2010) framed semi-arid floodplain resilience as a single state characterised by alternate dry and wet conditions. Broadly, our results fit a two-state boom-bust model because of the marked differences in vegetation productivity between the dry and wet resource states. The availability of water on the Narran floodplain, as noted by the area of floodplain inundation, differed between the DRS and WRS. There were marked differences in NDVI class area, number of transitions, direction of transitions, probability of transitions and NDVI class diversity between the dry phase and the combined wetting, wet and drying phases of floodplain inundation. This is related to the presence of water as a primary driver of floodplain vegetation productivity, where the arrival of floodwater stimulates a boom in production (Bunn *et al*., 2006) and may trigger recruitment or seed production (Capon, 2007). In contrast, the absence of water is associated with reduced vegetation production (Parsons and Thoms, 2013) and plant dormancy (Xu *et al*., 2010).

Division of the imagery into dry, wetting, wet and drying phases of floodplain inundation revealed complexity in vegetation productivity responses to resource availability. Most of the Narran floodplain was associated with low vegetation vigour during the dry phase, but the area and quality of vegetation vigour increased through the wetting and wet phases and decreased through the drying phase (Figure 3). None of the phases were stable, and there was always change between NDVI classes within a phase, with the greatest change between NDVI classes occurring in the wet phase (Figure 5). The ratio of single to two-way transitions was higher in the dry than the wetting, wet and drying phases combined (Figure 6). The dry phase had a platykurtic distribution of transition probabilities whereas the wetting, wet and drying phases had a bimodal distribution (Figure 7). These complex responses of vegetation to water availability are not unexpected. In a semi-arid floodplain ecosystem, Wen *et al*. (2012) reported that the interplay of flood size and flow path created a complex inundation pattern over time that was associated with complexity in NDVI response. Likewise, Parsons and Thoms (2013) examined the NDVI of Australian floodplain vegetation in wet, dry and rain resource states and concluded that NDVI values were varied and the spatio-temporal response was complex. Vegetation productivity responses within and between phases of flood inundation in our study suggest that complexity is related to a cycle of floodplain wetting and drying with different components of vegetation productivity responding differently to the availability of water.

In addition to the complexity of vegetation productivity through the dry, wetting, wet and drying phases of floodplain inundation, a distinct hysteretic loop was shown in the relationship between floodplain inundation and productivity (Figure 8 and Table 2). Hysteresis loops track the path of change in a system in response to external conditions and whether the system returns to its initial state or changes state (Nikanorov and Sukhoruhov, 2008; Searle *et al*., 2009). Vegetation productivity in the Narran floodplain consistently demonstrated a switch of direction during the wet phase of inundation. Most productivity measures also showed anti-clockwise hysteresis, and a flat trajectory (Table 2). Hysteretic patterns have been observed in semi-arid grassland response to grazing (Searle *et al*., 2009). Floodplain research by Murray *et al*. (2006) and Shilpakar (2013) has also reported hysteretic relationships between surface inundation and vegetation patchiness. Hysteresis in vegetation communities occurs when the return path to an original state differs from that taken during the degradation pathway (Searle *et al.*, 2009). The pattern of vegetation response to floodplain inundation observed in this study (Figure 8) indicates a hysteretic response of productivity to floodplain inundation through the dry, wetting, wet and drying phases.

We propose that this hysteretic pattern of vegetation productivity in response to floodplain inundation resembles an adaptive cycle. Thus, we derived a hypothesised adaptive cycle for the Narran floodplain where floodplain inundation drives vegetation responses through a cycle of exploitation, conservation, release and reorganization phases of an adaptive cycle (Figure 9). The adaptive cycle starts as floodwater inundates the floodplain in the wetting phase. The wetting phase corresponds to the exploitation part of the adaptive loop (Figure 9), where the area of vegetation productivity and its quality will increase because of the availability of water as an exploitable resource. Observed vegetation productivity responses during the wetting phase in the Narran floodplain were; a change in NDVI quality with NDVI moving from lower to higher classes; an increase in the number and direction of transitions between the different NDVI classes; and, an overall increase in the diversity of change in vegetation productivity (cf. Figures 3 and 5).

The wet phase is the phase of maximum floodplain inundation and corresponds to the conservation phase of the adaptive loop (Figure 9). The conservation phase is a period of increased vegetation productivity and stability of this productivity. Through the conservation phase vegetation biomass builds to its maximum because of ample water availability. During the wet phase vegetation productivity in the Narran floodplain was observed to be lower in terms of the area of vegetation productivity but higher in quality with a greater number of two-way directional transitions between NDVI classes (Figures 3 and 5). The wet or conservation phase was associated with an increase in vegetation productivity but lower stability.

The contraction of floodwater triggers the drying phase and corresponds to the release phase of an adaptive cycle (Figure 9). The release phase is an expected period of enhanced change triggered by internal or external agents of disturbances such as drought, fire or disease (Holling and Gunderson 2002). This phase initiates when tightly bound resources in vegetation and soil are released from the conservation phase and become a source for reorganization and renewal (Holling and Gunderson, 2002). During the drying phase in the Narran floodplain vegetation productivity was observed to decrease in area but the quality increased, as did the probability of change in vegetation productivity, the number of singular transitions and the overall diversity of NDVI class changes (Figures 3 and 5).

Further desiccation of the floodplain occurs with the draining of floodwaters until the floodplain reaches a dry phase; a phase of no surface water availability. The dry phase corresponds to the reorganization phase of the adaptive cycle. Reorganization is a critical phase of the adaptive cycle as it is during this phase that vegetation may reorganise into the same state as existed prior to the onset of wetting or the community may move to a new state in which case it is considered to have entered and “exit cycle” (Figure 9) (Holling and Gunderson, 2002; Scheffer and Carpenter, 2003). A decrease in the area of vegetation productivity and quality was expected in response to floodplain desiccation. However, during the dry phase in the Narran floodplain, the area of vegetation productivity increased but its quality declined. In addition decreases in two-way directions of change, the probability and diversity of change were observed (Figures 3 and 5) suggesting a period of stability (Figure 9).

The fore and back loops are key features of an adaptive cycle (Holling and Gunderson, 2002). The fore loop involves the exploitation to conservation phase of the adaptive loop and is characterized by stability and conservation (Holling and Gunderson, 2002; Walker and Salt 2006, 2012). The back loop involves the release to reorganization phase and is characterized by uncertainty, novelty and experimentation (Holling and Gunderson, 2002; Walker and Salt 2006, 2012). In our adaptive cycle of the Narran floodplain the fore loop is the wetting and wet phases between the exploitation and conservation phases. The fore loop in the Narran floodplain is characterised by higher vegetation productivity because of the availability of surface water. The back loop is the drying and dry phase between the release and reorganization phases, characterised in the Narran floodplain by change in vegetation productivity because of the withdrawal of energy and material associated with inundation. This arrangement of flooding as the fore loop and drying as the back loop of the adaptive cycle contrasts with the relatively simple single state model proposed by Colloff and Baldwin (2010) with the floodplain switching between the release (wet) and conservation (dry) phases only. Our results suggest greater complexity in the cycle of floodplain wetting and drying. The model of Colloff and Baldwin (2010) is not based on data but relies on their experience of floodplain soil carbon response in systems where the flow regime is highly regulated by dams and where floodplain inundation is more tightly coupled with managed flow releases. Riverine landscapes subject to highly variable and unpredictable flow regimes frequently display complex responses because of this variability (cf. Thoms, 2006). The Narran floodplain is a semi-arid system that experiences highly variable and unpredictable flow regimes (Thoms, 2003); the ecosystem response to which resembles an adaptive cycle.

The other key feature of an adaptive cycle is the change in the stability, or crossing of a threshold, where the system will flip in to a different regime while transitioning between the reorganization and exploitation phase (Scheffer and Carpenter, 2003). In our hypothesised floodplain adaptive cycle model we propose that such a flip may occur in the back loop transitioning between reorganization and exploitation phase or the dry phases of the floodplain adaptive cycle (Figure 9).

CONCLUSION

Despite the widespread acceptance of the theory of social-ecological resilience (Walker and Salt, 2012), there remains a relative paucity of empirical observations on one important component of resilience theory: the movement of systems through an adaptive cycle. Adaptive cycles of release and renewal have been demonstrated in economic systems, organizations, ecosystems and social systems (Alisson and Hobbs, 2004; Dearing, 2008; Burkhard *et al*., 2011; Walker and Salt, 2012). Our data suggests that adaptive cycles occur in semi-arid floodplain ecosystems in response to floodplain inundation. Adaptive cycles are a useful concept for understanding the complexity of semi-arid floodplain ecosystem responses to inundation. Maintaining the natural variability of floodplain inundation is a key ecological management issue because variability in the wetting and drying of semi-arid floodplains maintains their resilience (Colloff and Baldwin, 2010; Baldwin *et al*., 2013b). However, change in climate and land and water resource development activities has reduced the natural variability of floodplain inundation and may worsen in the future (Thoms and Sheldon, 2000; Erwin, 2009). Adaptive cycles make us more cognizant of the importance of transitions, dominance of the different phases, and the frequency of the individual transitions driving ecosystem change. Knowledge of the phases of vegetation response around an adaptive cycle will enable better management of floodplains because management activities can be tailored to specific phases or used to push vegetation through different phases (Colloff and Baldwin, 2010; Walker and Salt, 2012).

ACKNOWLEDGEMENTS

We thank Dr Michael Reid for his helpful comments on the manuscript. This research was supported by a UNE International Strategic Post Graduate Scholarship. Finally, we would like to thank Geoscience Australia and USGS for the Landsat images.

REFERENCES

Allison HE, Hobbs RJ. 2004. Resilience, adaptive capacity, and the lock-in trap of the Western Australian agricultural region. *Ecology and Society* **9**:3. http://www.ecologyandsociety.org/vol9/iss1/art3/

Arthington AH, Olden JD, Balcombe SR, Thoms MC. 2010. Multi-scale environmental factors explain fish losses and refuge quality in drying waterholes of Cooper Creek, an Australian arid-zone river. *Marine and Freshwater Research* **61**: 842-856. DOI: 10.1071/MF09096

Balcombe SR, Arthington AH. 2009. Temporal changes in fish abundance in response to hydrological variability in a dryland floodplain river. *Marine and Freshwater Research* **60**: 146-159. DOI:10.1071/MF08118

Balcombe SR, Bunn SE, Arthington AH, Fawcett JH, McKenzie-Smith FJ, Wright A. 2007. Fish larvae, growth and biomass relationships in an Australian arid zone river: links between floodplains and waterholes. *Freshwater Biology* **52**: 2385-2398. DOI: 10.1111/j.1365-2427.2007.01855.x

Baldwin D, Rees G, Wilson J, Colloff M, Whitworth K, Pitman T, Wallace T. 2013a. Provisioning of bioavailable carbon between the wet and dry phases in a semi-arid floodplain. *Oecologia* **172**: 539-550. DOI: 10.1007/s00442-012-2512-8

Baldwin DS, Colloff MJ, Rees GN, Chariton AA, Watson GO, Court LN, Hartley DM, Morgan Mj, King AJ, Wilson JS, Hodda M, Hardy CM. 2013b. Impacts of inundation and drought on eukaryote biodiversity in semi-arid floodplain soils. *Molecular Ecology* **22**: 1746-1758. DOI: 10.1111/mec.12190

Baldwin DS, Mitchell AM. 2000. The effects of drying and re-flooding on the sediment and soil nutrient dynamics of lowland river–floodplain systems: a synthesis. *Regulated Rivers: Research & Management* **16**: 457-467. DOI: 10.1002/1099-1646

Bolliger J, Wagner HH, Turner MG. 2007. Identifying and quantifying landscape patterns. In: *A Changing World. Challenges for Landscape Research*. Kienast F, Wildi O, Ghosh S (eds). Springer Science: 177-194. Dordrecht, The Netherlands.

Bunn SE, Thoms MC, Hamilton SK, Capon SJ. 2006. Flow variability in dryland rivers: boom, bust and the bits in between. *River Research and Applications* **22**: 179-186. DOI: 10.1002/rra.904

Burkhard B, Fath BD, Müller F. 2011. Adapting the adaptive cycle: Hypotheses on the development of ecosystem properties and services. *Ecological Modelling* **222**: 2878-2890. DOI: 10.1016/j.ecolmodel.2011.05.016

Capon SJ. 2003. Plant community responses to wetting and drying in a large arid floodplain. *River Research and Applications* **19**: 509- 520. DOI:10.1002/rra.730

Capon SJ. 2007. Effects of flooding on seedling emergence from the soil seed bank of a large desert floodplain. *Wetlands* **27**: 904-914. DOI: 10.1672/0277-5212

Chander G, Markham BL, Helder DL. 2009. Summary of current radiometric calibration coefficients for Landsat MSS, TM, ETM+, and EO-1 ALI sensors. *Remote Sensing of Environment* **113**: 893-903. DOI: 10.1016/j.rse.2009.01.007

Colloff MJ, Baldwin DS. 2010. Resilience of floodplain ecosytems in a semi-arid environment. *The Rangeland Journal* **32**: 305-314. DOI:10.1071/RJ10015

Dearing J. 2008. Landscape change and resilience theory: a palaeoenvironmental assessment from Yunnan, SW China. *The Holocene* **18**: 117-127. DOI:10.1177/0959683607085601

Erwin KL. 2009. Wetlands and global climate change: the role of wetland restoration in a changing world. *Wetlands Ecology and management* **17**: 71-84.DOI:10.1007/s11273-008-9119-1

Farina A. 2006. *Principles and Methods in Landscape Ecology: Towards a Science of Landscape*. Springer: Dordrecht, The Netherlands.

Fitzpatrick A, Clarke JDA, Lane R. 2005. Mapping hydrological architecture beneath the lower Balonne floodplain, Queensland, Australia. *Geophysical Research Abstracts* **7**: 02505.

Folke C,Carpenter SR, Walker B, Scheffer M, Chapin T, Rockström J. 2010. Resilience Thinking: integrating resilience, adaptability, and transformability. *Ecology and Society* **15**: 20. http://www.ecologyandsociety.org/vo15/iss4/art20/

Frazier PS, Page KJ. 2000. Water body detection and delineation with Landsat TM data. *Photogrammetric Engineering and Remote Sensing* **66**: 1461-1468.

Holling CS. 1973. Resilience and stability of ecological systems. *Annual Reiew of Ecology and Systematics* **4**:1-23.DOI:10.1146/annurev.es.04.110173.000245

Holling CS, Gunderson L. 2002. Resilience and adaptive cycles. In *Panarchy: Understanding Tranformations in Human and Natural Systems*. Gunderson L, Holling CS (eds). Island Press: Washington DC: 25-62.

Kingsford R, Curtin A, Porter J. 1999. Water flows on Cooper Creek in arid Australia determine 'boom'and 'bust'periods for waterbirds. *Biological Conservation* **88**: 231-248. DOI:10.1016/s0006-3207(98)00098-6

Leigh C, Sheldon F, Kingsford RT, Arthington AH. 2010. Sequential floods drive 'booms' and wetland persistence in dryland rivers: a synthesis. *Marine and Freshwater Research* **61**: 896-908.

Lillesand TM, Kiefer RW. 2000. *Remote Sensing and Image Interpretation*. John Wiley & Sons: New York.

Magurran AE. 1988. *Ecological Diversity and its Measurement*. Chapman and Hall: UK.

Murray O, Thoms M, Rayburg S, 2006. The diversity of inundated areas in semi-arid flood plain ecosystems. *International Association of Hydrological Sciences,* Publication Number **306**: 277-286.

Myeong S, Nowak DJ, Duggin MJ. 2006. A temporal analysis of urban forest carbon storage using remote sensing. *Remote Sensing of Environment* **101**: 277-282. DOI:10.1016/j.rse.2005.12.001

Nikanorov AM, Sukhoruhov BL. 2008. Ecological hysteresis. *Doklady Earth Sciences* **423**:1282-1285.DOI:10.1134/S1028334X08080229

Overton IC. 2005. Modelling floodplain inundation on a regulated river: integrating GIS, remote sensing and hydrological models. *River Research and Applications* **21**: 991-1001. DOI:10.1002/rra.867.

Parsons M, Thoms MC. 2013. Patterns of vegetation greenness during flood, rain and dry resource states in a large, unconfined floodplain landscape. *Journal of Arid Environments* **88**: 24-38. DOI:10.1016/j.jaridenv.2012.07.023.

Puckridge JT, Walker KF, Costelloe JF. 2000. Hydrological persistence and the ecology of dryland rivers. *Regulated Rivers: Research & Management* **16**: 385-402. DOI: 10.1002/1099-1646

Rayburg S, Thoms M. 2009. A coupled hydraulic–hydrologic modelling approach to deriving a water balance model for a complex floodplain wetland system. *Hydrology Research* **40**: 364-379. DOI:10.2166/nh.2009.110

Rayburg S, Thoms M, Lenon E. 2006. Unravelling the physical template of a terminal floodplain - wetland sediment storage system. *Sediment Dynamics and the Hydromorphology of Fluvial Systems, Proceeding of a Symposium held in Dundee, UK.* Publication Number **306**: IAHS Press, Wallingford: 304-313.

Reid MA, Ogden R, Thoms MC. 2011. The influence of flood frequency, geomorphic setting and grazing on plant communities and plant biomas on a large dryland floodplain. *Journal of Arid Environments* **75:** 815–826. DOI: 10.1016/j.jaridenv.2011.03.014

Roshier DA, Robertson AI, Kingsford RT. 2002. Responses of waterbirds to flooding in an arid region of Australia and implications for conservation. *Biological Conservation* **106**: 399-411. DOI:10.1016/S0006-3207(01)00268-3

Scheffer M, Carpenter SR. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology & Evolution* **18**: 648-656. DOI: 10.1016/j.tree

Schröder A, Persson L, De Roos AM. 2005. Direct experimental evidence for alternative stable states: a review. *Oikos* **110**: 3-19. DOI:10.1111/j.0030-1299.2005.13962.x

Schwinning S, Sala OE. 2004. Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. *Oecologia* **141**: 211-220. DOI:10.1007/s00442-004-1520-8

Searle KR, Gordon IJ, Stokes CJ. 2009. Hysteretic Responses to grazing in a semiarid rangeland. *Rangeland Ecology & Management* **62**: 136-144. DOI: 10.2111/08-200.1

Shaikh M, Green D, Cross H. 2001. A remote sensing approach to determine environmental flows for wetlands of the Lower Darling River, New South Wales, Australia. *International Journal of Remote Sensing* **22**: 1737-1751. DOI:10.1080/01431160118063

Shilpakar RL. 2013. *Floodplain Vegetation Landscapes: An Ecotone or a Dynamic Patch Mosaic?*. PhD Thesis, University of New England, Armidale.

Sims NC, Thoms MC. 2002. What happens when flood plains wet themselves: vegetation response to inundation on the lower Balonne floodplain. *International Association of Hydrological Sciences,* Publication Number **276**: 195- 202.

Smith MD, Knapp AK, Collins SL. 2009. A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. *Ecology* **90**: 3279-3289. DOI:10.1890/08-1815.1

Thoms MC, Sheldon F. 2000. Water resource development and hydrological change in a large dryland river: the Barwon–Darling River, Australia. *Journal of Hydrology* **228**: 10-21.DOI:10.1016/s0022-1694(99)00191-2

Thomas R, Bowen S, Simpson S, Cox S, Sims N. 2010. Innundation response of vegetation communities of the Macquarie Marshes in semi-arid Australia. In: *Ecosystem Response Modelling in the Murray-Darling Basin*. Saintilan N, Overton I (eds). CSIRO publishing, Melbourne.

Thoms M, Capon S, James C, Padgham M, Rayburg S. 2007. *The Narran Ecosystem Project: The Response of a Terminal Wetland System to Variable Wetting and Drying*. Final report to the Murray-Darling Basin Commision. MDBC Publication No.40/08. Canberra, Australia.

Thoms MC. 2006. Variability in riverine ecosystems. *River Research and Application* **22**: 115 - 121. DOI:10.1002rra.900

Thoms MC. 2003. Floodplain-river ecosystems: lateral connections and the implications of human interference. *Geomorphology* **56**: 335-349. DOI: 10.1016/s0169-555x(03)00160-0

Walker B, Salt D. 2012. *Resilience Practice: Building Capacity to Absorb Disturbance and Maintain Function*. Island Press: Washington DC.

Walker B, Salt D. 2006. *Resilience Thinking. Sustaining Ecosystems and People in a Changing World*. Island Press: Washington DC.

Walker KF, Sheldon F, Puckridge JT. 1995. A perspective on dryland river ecosystems. *Regulated Rivers: Research & Management* **11**: 85-104. DOI: 10.1002/rrr.3450110108

Wen L, Yang X, Saintilan N. 2012. Local climate determines the NDVI-based primary productivity and flooding creates heterogeneity in semi-arid floodplain ecosystem. *Ecological Modelling* **242**: 116-126. DOI: 10.1016/j.ecolmodel.2012.05.018

Weng Q. 2002. Land use change analysis in the Zhujiang Delta of China using satellite remote sensing, GIS and stochastic modelling. *Journal of Environmental Management* **64**: 273-284. DOI:10.1006/jema.2001.0509

Westbrooke ME, Florentine SK, Milberg P. 2005. Arid land vegetation dynamics after a rare flooding event: influence of fire and grazing. *Journal of Arid Environments* **61**: 249-260. DOI: 10.1016/j.jaridenv.2004.09.004

Whalley R, Price J, Macdonald M, Berney P. 2011. Drivers of change in the social ecological systems of the Gwydir Wetlands and Macquarie Marshes in northern New South Wales, Australia. *The Rangeland Journal* **33**: 109-119.DOI :10.1071/RJ11002

Xu H. 2006. Modification of normalised difference water index (NDWI) to enhance open water features in remotely sensed imagery. *International Journal of Remote Sensing* **27**: 3025-3033. DOI:10.1080/01431160600589179

Xu Z, Zhau G, Shimizu H. 2010. Plant responses to drought and rewatering. *Plant Signal Behaviour* **5**: 649-654.

Table 1. Satellite images comprising the dry and wet resource states, with corresponding hydrology, rainfall and temperature conditions. A period refers to the comparison of two images, where the comparison of image 1 and 2 becomes period 1.

Date of image	Image number	Period	Total flow (ML)	Total monthly rainfall (mm)	Mean monthly maximum temperature (°C)
Dry resource state					
20-01-2002	1		0	0	37.0
05-02-2002	2	1	0	30.0	34.2
09-03-2002	3	2	0	4.0	33.3
10-04-2002	4	3	0	34.0	29.8
28-05-2002	5	4	997	0	23.3
29-06-2002	6	5	6	17	20.0
15-07-2002	7	6	0	0	20.4
16-08-2002	8	7	0	12.0	22.5
17-09-2002	9	8	0	19.0	26.2
19-10-2002	10	9	0	7.0	31.3
04-11-2002	11	10	0	6.0	36.7
06-12-2002	12	11	0	15.0	35.5
Wet resource state					
18-01-2004	13		8679	104.0	35.6
03-02-2004	14	12	18199	26.0	36.1
19-02-2004	15	13	18199	123.0	36.1
23-04-2004	16	14	407	27.0	29.1
09-05-2004	17	15	0.44	25.0	21.6
10-06-2004	18	16	0	10.0	19.7
12-07-2004	19	17	0	31.0	17.9
14-09-2004	20	18	0	19.0	24.9
16-10-2004	21	19	0	15.0	30.2
17-11-2004	22	20	0	108.0	32.0
19-12-2004	23	21	1115	107.0	33.1

Table 2. Pattern of cyclic change in vegetation productivity measures in response to floodplain inundation. For hysteresis direction AC = anti-clockwise and C = clockwise. Example hysteresis loops are given in Figure 8.

Response pattern	Vegetation productivity measure														
	Change in NDVI class area					Number of transitions	Direction of transition		Probability of transition						Diversity of change
	NDVI 2	NDVI 3	NDVI 4	NDVI 5	NDVI 6		Single	Multi	<1	1-5	5-10	10-20	20-50	>50	
Hysteresis direction	C	AC	AC	AC	AC	AC	C	AC	AC	C	AC	AC	AC	AC	C
Phase of switch	Wet	Wet	Wet	Wet	Wet	Wet	Wet	Wet	Wet	Wet	Wet	Wet	Wet	Wet	Wet
Shape of switch	Flat	Flat	Steep	Steep	Steep	Flat	Flat	Steep	Steep	Flat	Flat	Flat	Flat	Flat	Flat

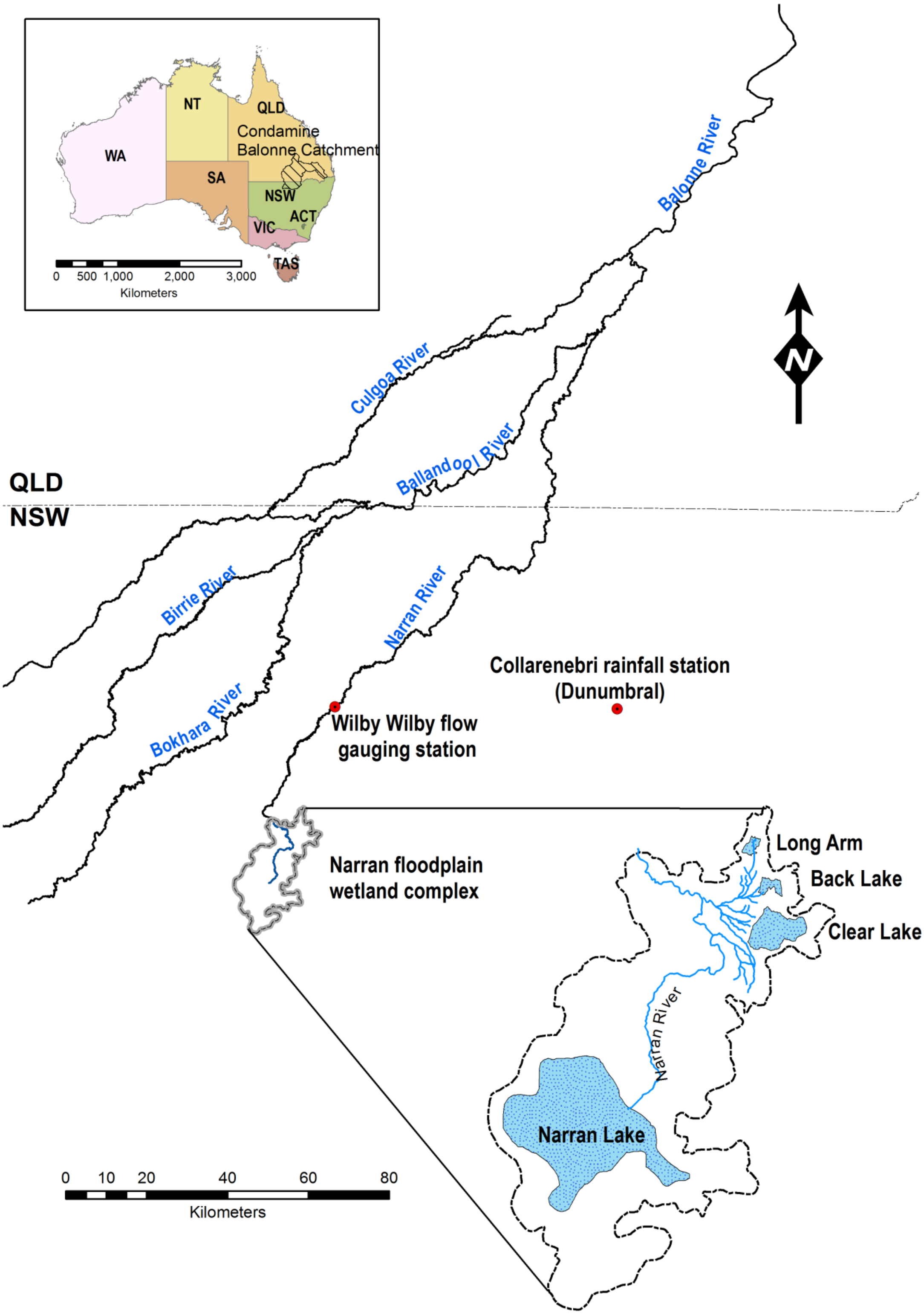


Figure 1. Location of the Narran floodplain within the lower reaches of the Condamine-Balonne River catchment.

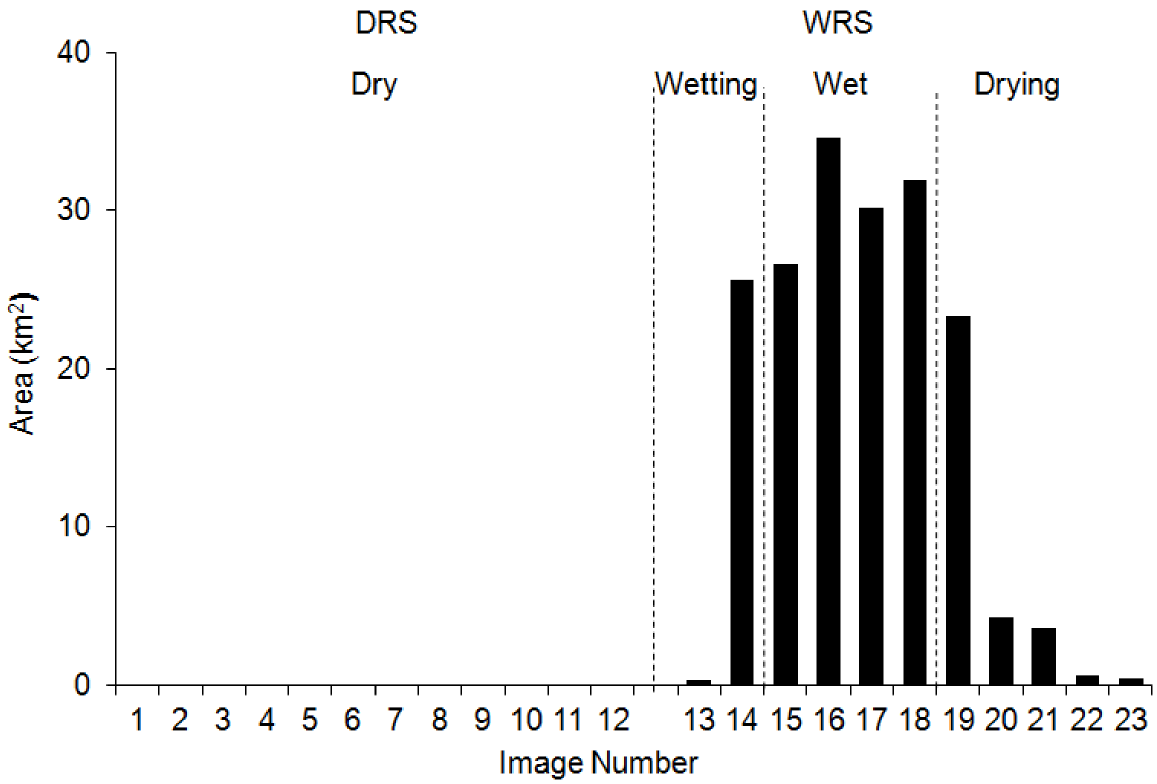


Figure 2. Area of floodplain inundation during the dry and wet resource states. The wet resource state is further divided into wetting, wet and drying phases. Image numbers are explained in Table 1.

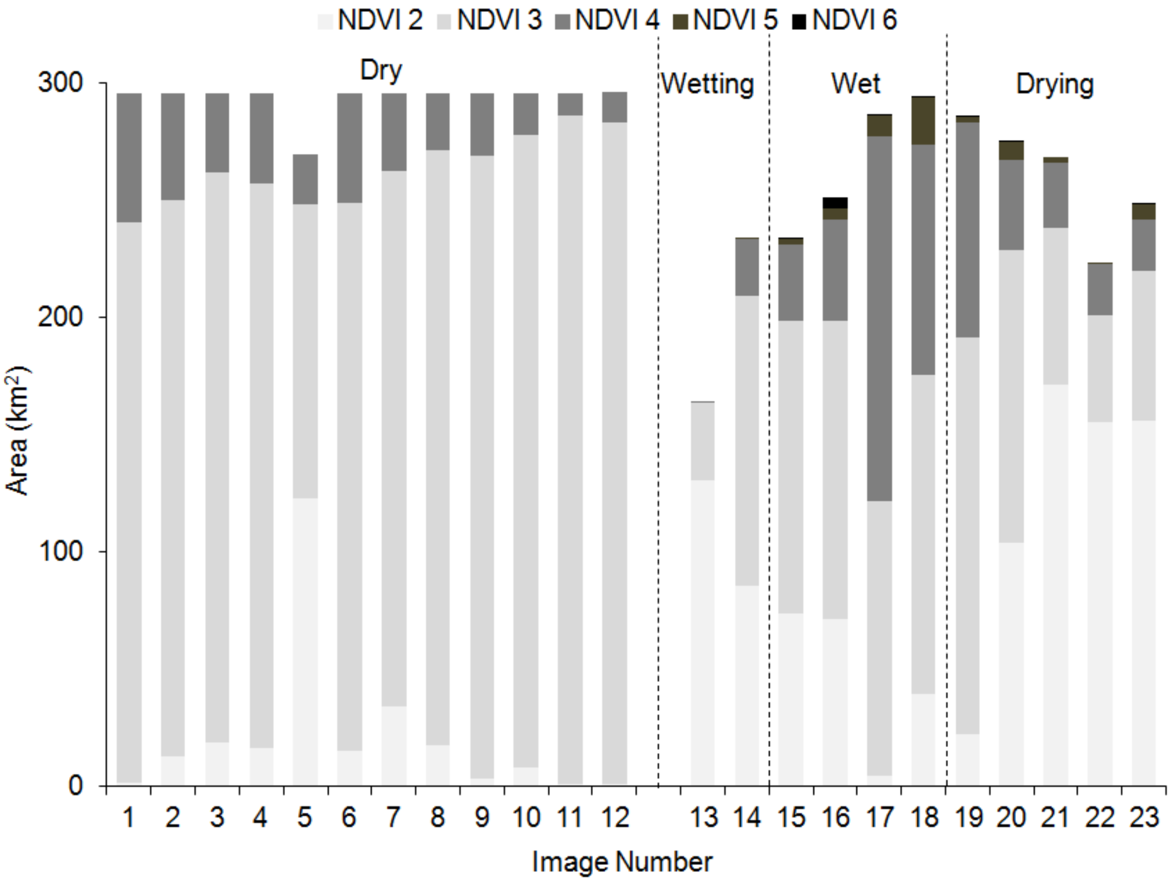


Figure 3. Area of NDVI Classes 2-6 in the Narran floodplain in the dry, wetting, wet and drying phases of inundation. NDVI Class 1 is not shown because it represents bare ground or water. Image numbers are explained in Table 1.

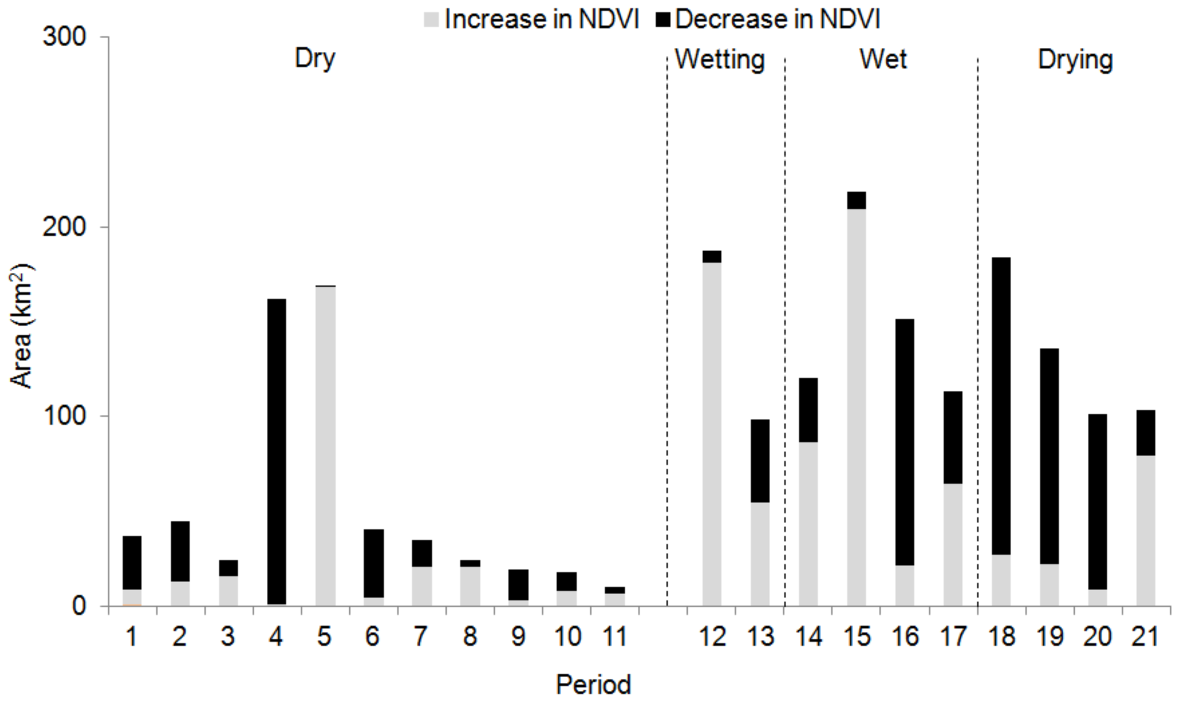


Figure 4. Area of floodplain change among six NDVI classes for the dry, wetting, wet and drying phases of inundation. Floodplain change is divided into the area that increased or decreased in NDVI class between consecutive images. Periods are explained in Table 1.

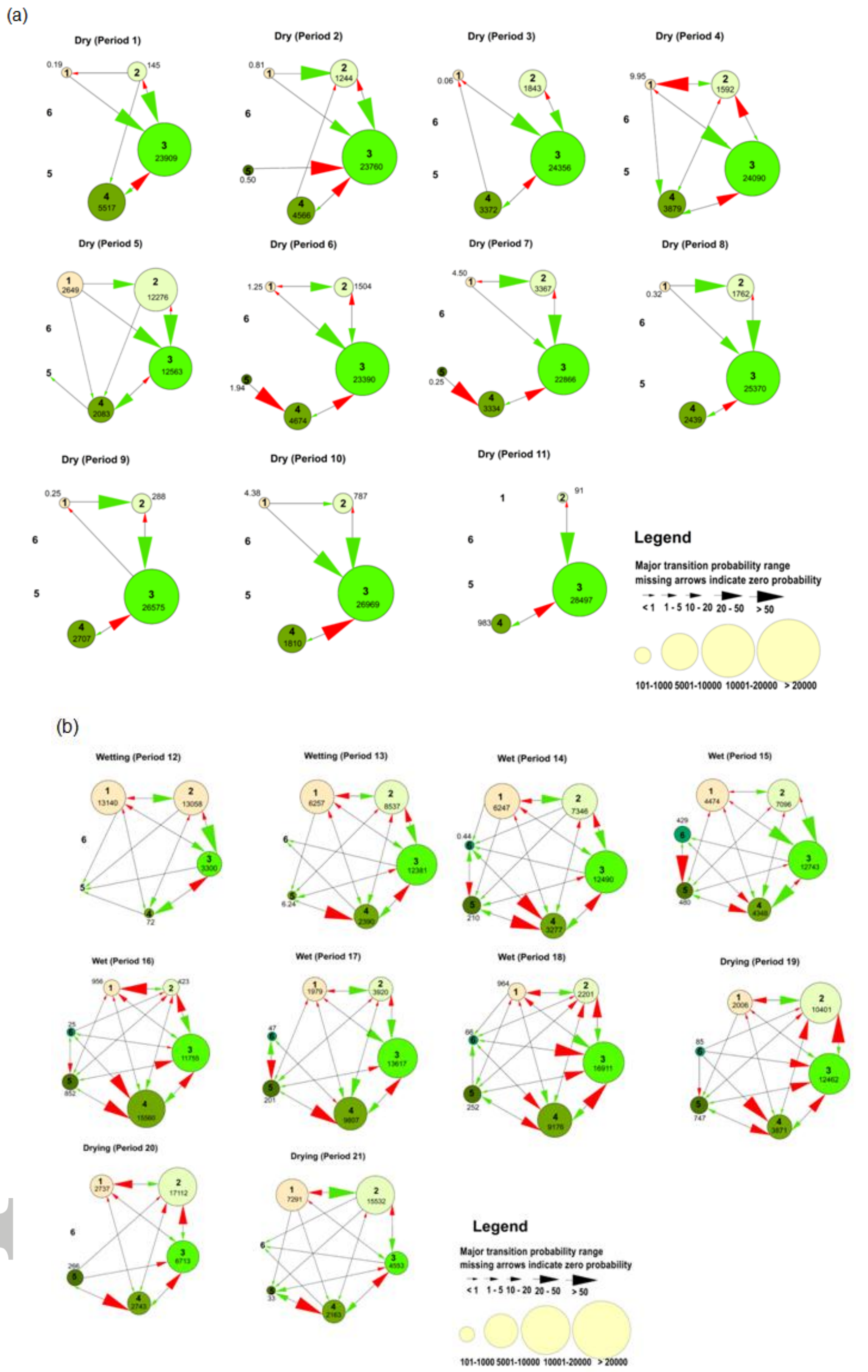


Figure 5. Markovian transition models of change between NDVI classes 1-6 in the dry (a) and wetting, wet and drying (b) phases of floodplain inundation. The area of floodplain in each NDVI class is shown by different sized circles, and labelled with area (ha). Arrows identify the changes between NDVI classes, where red arrows indicate decrease and all the green arrows showed increase in NDVI classes. The size of the arrowhead indicates the probability of change among NDVI classes. Periods are explained in Table 1.

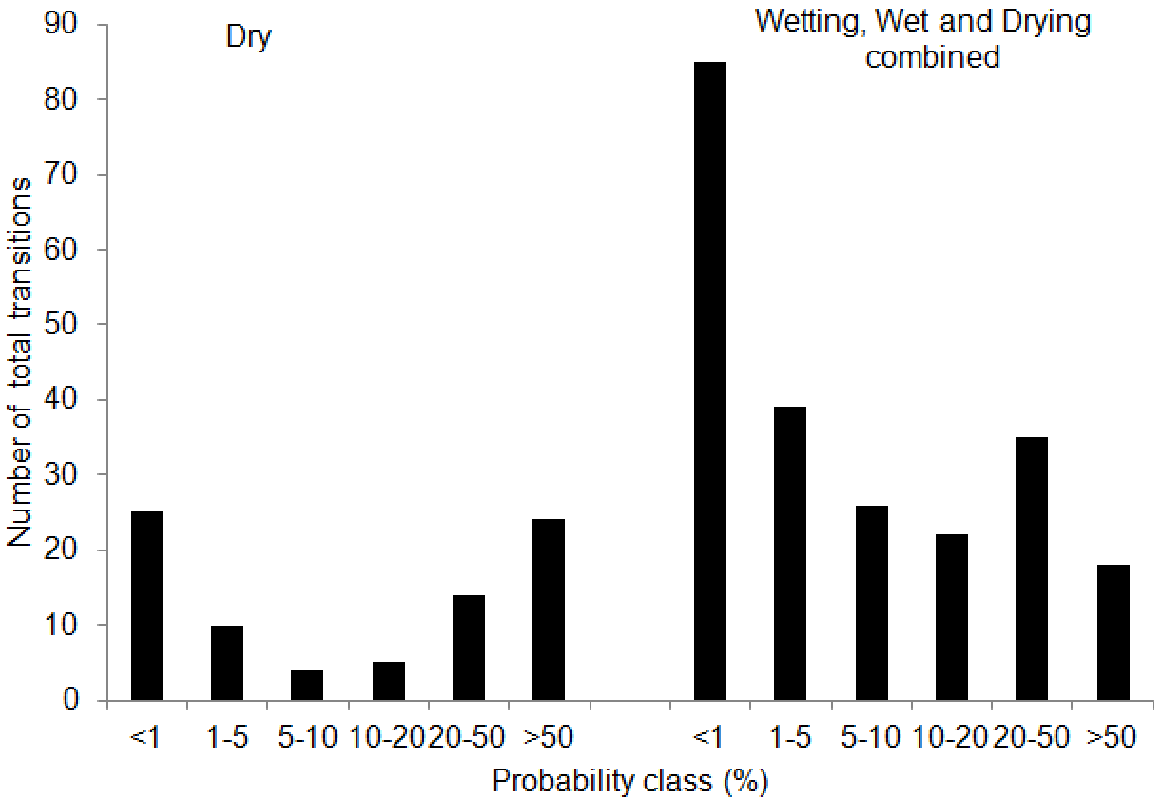


Figure 6. Distribution of the probability of transitions between all NDVI classes in the dry and combined wetting, wet and drying phases of flood inundation. Probability transitions were tallied from the Markovian transition models shown in Figure 5.

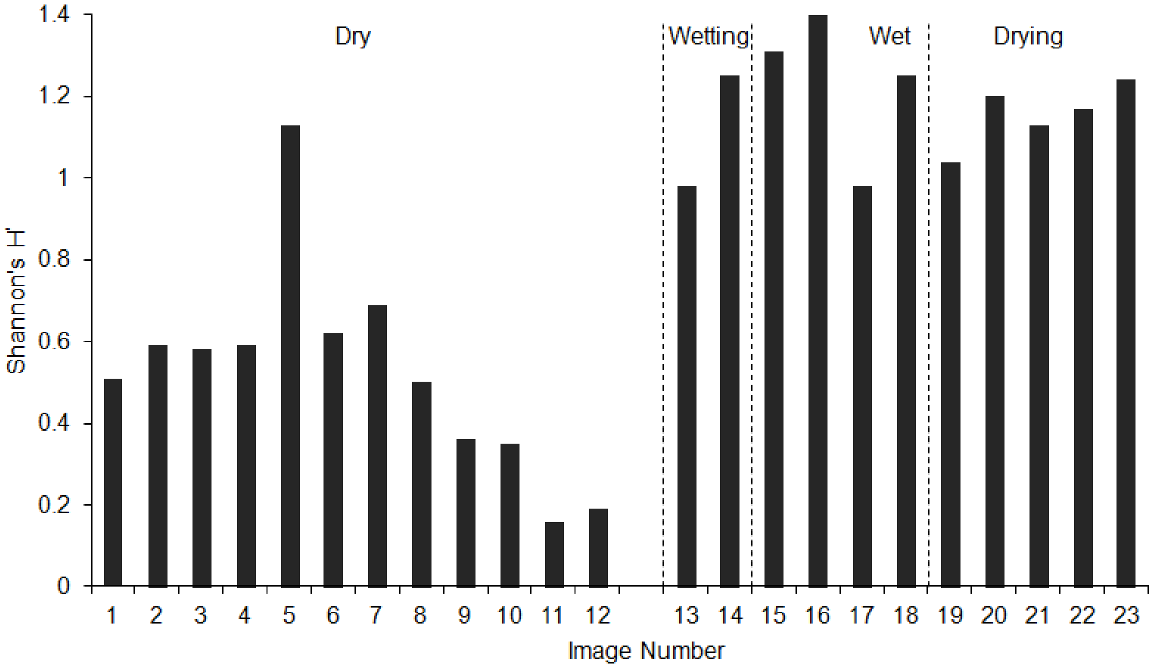


Figure 7. Shannon-Wiener Diversity Index of change in NDVI classes 2-6 for the dry, wetting, wet and drying phases. Images are explained in Table 1.

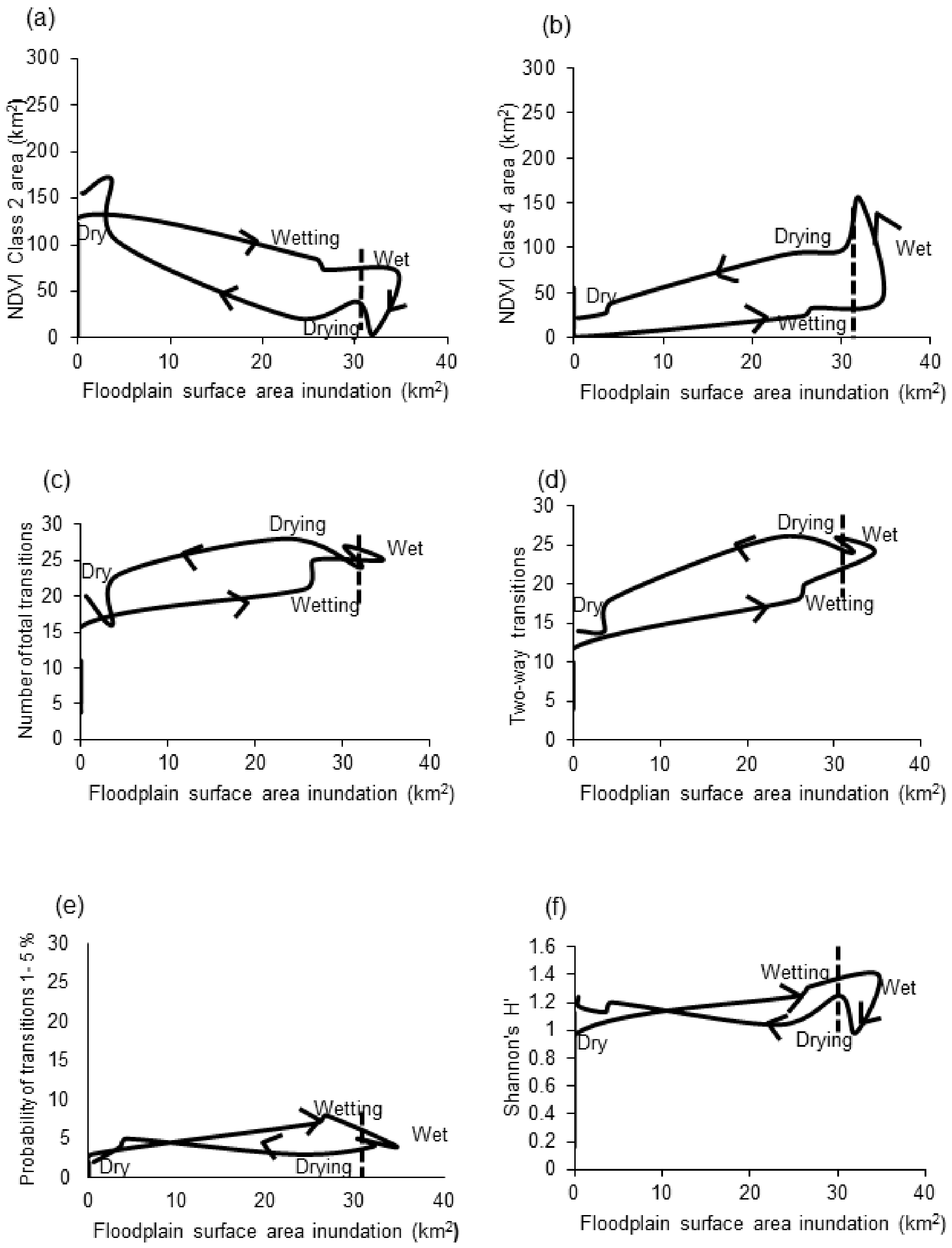
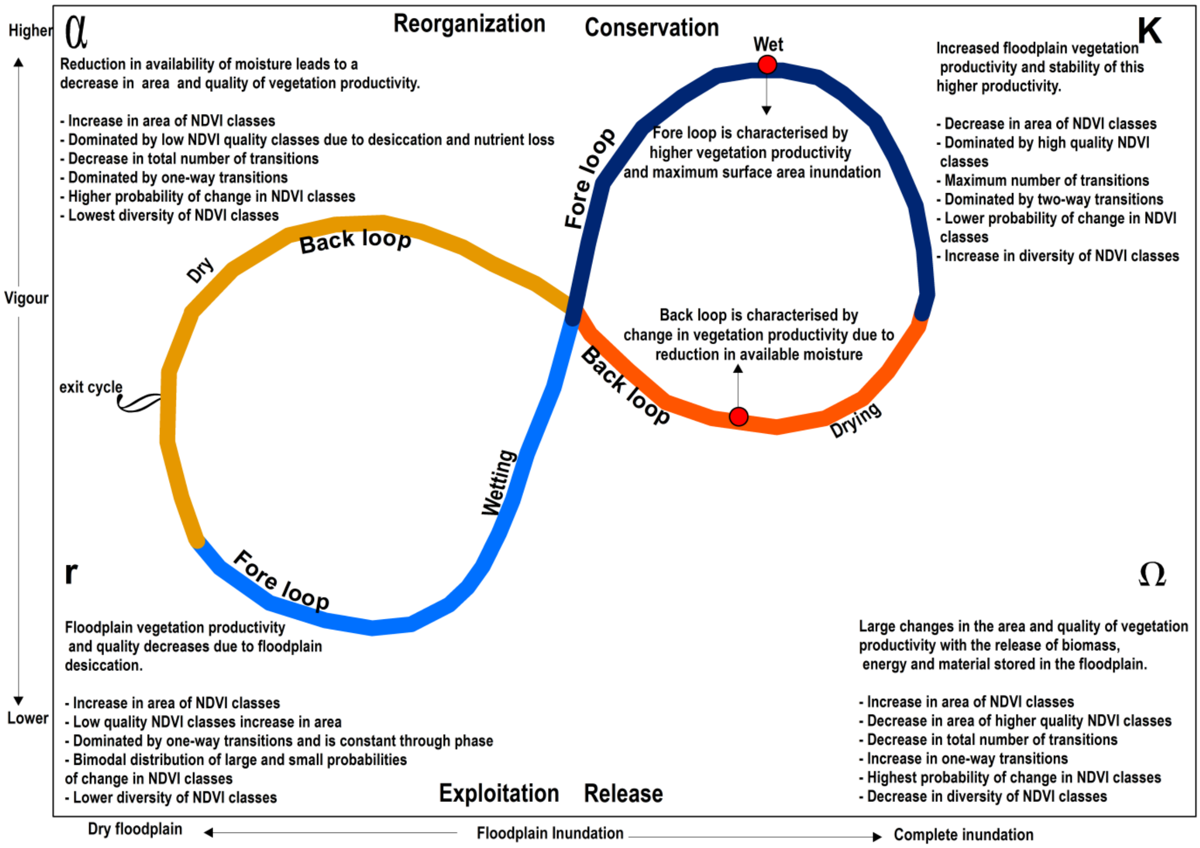


Figure 8. Cyclic change in (a) NDVI Class 2 area, (b) NDVI Class 4 area, (c) total number of transitions, (d) multiple transitions (one-way or two-way transitions), (e) transition probability 1-5 % and (f) diversity in relation to floodplain inundation. The dry, wetting, wet and drying phases correspond to the phases of floodplain inundation outlined in Figure 2.



Reduction in availability of moisture leads to a decrease in area and quality of vegetation productivity.

- Increase in area of NDVI classes
- Dominated by low NDVI quality classes due to desiccation and nutrient loss
- Decrease in total number of transitions
- Dominated by one-way transitions
- Higher probability of change in NDVI classes
- Lowest diversity of NDVI classes

Fore loop is characterised by higher vegetation productivity and maximum surface area inundation

Increased floodplain vegetation productivity and stability of this higher productivity.

- Decrease in area of NDVI classes
- Dominated by high quality NDVI classes
- Maximum number of transitions
- Dominated by two-way transitions
- Lower probability of change in NDVI classes
- Increase in diversity of NDVI classes

Back loop is characterised by change in vegetation productivity due to reduction in available moisture

Floodplain vegetation productivity and quality decreases due to floodplain desiccation.

- Increase in area of NDVI classes
- Low quality NDVI classes increase in area
- Dominated by one-way transitions and is constant through phase
- Bimodal distribution of large and small probabilities of change in NDVI classes
- Lower diversity of NDVI classes

Large changes in the area and quality of vegetation productivity with the release of biomass, energy and material stored in the floodplain.

- Increase in area of NDVI classes
- Decrease in area of higher quality NDVI classes
- Decrease in total number of transitions
- Increase in one-way transitions
- Highest probability of change in NDVI classes
- Decrease in diversity of NDVI classes

Figure 9. The hypothesised adaptive cycle model of the Narran floodplain based on hydrology and vegetation productivity.