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Patch organisation and resilience of dryland wetlands

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Abstract

Dryland wetlands are ecosystems of high ecological importance as they serve as habitat sanctuaries for aquatic and terrestrial biota in areas with very few resources; therefore, the study of such environments is of major importance for the conservation of biodiversity in arid and semi-arid areas. The vegetation organization in these ecosystems is driven by the water regime as the main driver, but local processes like seed banks and soil resources redistribution also play a crucial role in determining the spatial distribution of the vegetation. Assessment of vegetation dynamics and long-term resilience requires the use of realistic models that can integrate the water regime and that can continuously simulate vegetation extent and conditions under flood-drought cycles. Here we study the influence of the water regime as the main driver of the vegetation. We apply a vegetation-modelling framework to compare the performance of a simplified model at the cell scale and a model integrated at a patch scale. Our results show that aggregating the analysis of vegetation dynamics at the patch scale allows for the incorporation of the effects of both local drivers (acting within the patch) as well as the global drivers (acting over the patch as a whole). The water regime acts as a global driver for the vegetation and indirectly affects the local drivers. Our patch scale model successfully captures wetland vegetation dynamics using the water regime as the main driver for representing changes in the vegetation and assessment of the wetland resilience under flood-drought periods.

Keywords

vegetation dynamics, dryland wetlands, wetland modelling, wetland resilience

1. Introduction

Vegetation zonation and patch differentiation are common vegetation spatial features of many landscapes. One of such landscapes is the floodplain wetlands in dryland zones, where plant community distribution is the result of complex hydrological and geomorphological processes. The interplay of surface water flow and topography results in inundation patterns (often described as the water regime), which dictate the water available for plant use. The water regime can be described by the inundation frequency, depth, and duration and is recognised as one of the main drivers of vegetation establishment, composition and change (Casanova and Brock, 2000, Roberts and Marston, 2011, Webb et al., 2012). Periodical transitions between different vegetation states of plant dominance or health conditions (referred to as vegetation dynamics in this study), can respond to global drivers such as the water regime acting over the domain of the study, but other local feedback processes or site characteristics are also drivers of the spatial structure of vegetation communities at a smaller scale (Foti et al., 2013, Foti et al., 2012). Factors such as seed bank availability (Capon and Brock, 2006, Pueyo et al., 2008), salinity (Porter et al., 2007, Pennings et al., 2005), soil moisture (Rodriguez-Iturbe et al., 2007), fire frequency (Davis et al., 2002), and inter-species competition (Keddy and Fraser, 2000, Pennings et al., 2005) can have strong influences on vegetation establishment. These local drivers are more prevalent in landscapes with limited water availability or where periodical flooding does not completely dominate vegetation establishment. For example, trees and grass cluster structures in savannahs are driven by soil moisture, bushfires, and competition between grass and trees (Yu and D'Odorico, 2014, Rodriguez-Iturbe et al., 2019). In flood-dominated environments, distinguishing between global and local drivers can be challenging because the vegetation spatial organization is the result of the combination of several drivers (Marani et al., 2013, D’Odorico et al., 2011).

Representation of global and local drivers in vegetation dynamics and hydro-geomorphic models is often done using rules-based cellular automata models (Solari et al., 2016, Saco and Rodríguez, 2013). In some cases, the local feedback processes are linked to the global drivers, allowing for a deterministic analysis of the vegetation using the water regime as the main driver of the vegetation patterns. In recent studies of coastal wetlands around the globe, a mechanical characterization of the tidal water regime has allowed to simulate saltmarsh and mangrove dynamics (Marani et al., 2007, D'Alpaos et al., 2007, Fagherazzi et al., 2012, van Maanen et al., 2015, Belliard et al., 2015, Alizad et al., 2016, Kirwan et al., 2016, Rodríguez et al., 2017, Sandi et al., 2018). In freshwater wetlands, the water regime is the result of multiple hydrological processes occurring at the catchment level. This often results in highly variable water regimes where local drivers have a more significant role in the vegetation dynamics and the formation of vegetation patches (D’Odorico et al., 2011, Foti et al., 2013). From a modelling perspective, additional functions must be included to integrate local processes, which adds complexity to the models and requires additional data collection for calibration and model testing. Despite the importance of local drivers, the water regime still plays a significant role in the distribution of vegetation of freshwater wetland systems (Dong et al., 2016, Pettit et al., 2001) and it provides the basis for alternative stable vegetation patterns or patches (Suding et al., 2004, Heffernan, 2008). Vegetation in dryland wetlands is highly resilient and capable of surviving flood-drought periods due to different strategies linked to the water regime such as seed and rhizome bank maintenance, resources redistribution, and dormancy mechanisms (Capon and Reid, 2016, Capon and Brock, 2006).

Here, we study the influence of local drivers (influenced by global drivers) on the organization of vegetation into vegetation patches, and the response of those patches to the water regime spatially aggregated over the patch. We apply this framework to an iconic dryland wetland located in semiarid Australia, integrating continuously varying water regime and water preferences of six different vegetation stable states. The water regime is simulated with a two-dimensional hydrodynamic model where vegetation patches are represented as areas with different roughness coefficients. When vegetation changes to a different state, roughness also changes, incorporating a feedback mechanism into the model. For each patch of vegetation the spatially averaged water regime is represented with the Minimum Inundation Index (MII) (Sandi et al., 2019), in combination with simple functions that represent competition between wetland species and terrestrial vegetation or changes in the state of the vegetation health. We compare this approach to computing changes in the vegetation considering the same rules for a cellular automata model that only considers global drivers.

Patch organisation is a recognised feature of dryland wetland vegetation, but it has not been formally incorporated into a simulation and prediction tool before. The novelty of our patch approach consists of integrating the water regime and the footprint of the observed vegetation patch organisation to indirectly incorporate local drivers into the simulation. The use of a discrete patch distribution and the water regime as a global driver provides a better representation of changes in the vegetation and assessment of the wetland resilience under flood-drought cycles. Our approach is much more practical than the alternative of explicitly simulating all local drivers and can be easily extended to other wetland systems without requiring extensive detailed information.

2. Materials and Methods

We applied our two vegetation dynamics models, the cellular automata with no local drivers and the patch model, to the Northern Marshes of the Macquarie Marshes, located in the lowland floodplain of the Macquarie River, Australia (Figure 1). This wetland has a semiarid climate and receives most of its water from upstream catchments, including environmental releases from the nearby Burrendong Dam. Extensive non-woody vegetation communities of Common reed (*Phragmites australis*), Water couch (*Paspallum distichum*) and Mixed marsh (*Juncus sp, Paspallum distichum, Phragmites* *australis, Typha sp.*), as well as woody vegetation communities such as River red gum (*Eucalyptus camaldulensis*) provide unique habitat to a large number of invertebrates (e.g. frogs and turtles), birds and fish. Vegetation surveys carried out in 1991 (Wilson, 1992), 2008 and 2013 (Bowen et al., 2017) showed important transformations in the distribution of vegetation. Between 2001 and 2009, the vegetation suffered significant deterioration due to the effects of extended drought conditions, the Millennium Drought. In 2008, areas of non-woody vegetation were reported to transition to terrestrial vegetation and areas of woody vegetation were reported to be in poor conditions (more than 80% of trees showing apparent mortality). After the break of the drought in 2010 and record-breaking rainfall in the following years, vegetation recovery was reported in 2013 (Bowen et al., 2017). The vegetation dynamics model has been developed to simulate these drying scenario transitions of non-woody vegetation to terrestrial vegetation and the condition of woody vegetation between 1991 and 2013. We first simulate the water regime with a spatially distributed hydrodynamic model and then combine a series of rules describing vegetation preferences to determine the extent of non-woody vegetation and woody vegetation conditions in the site.

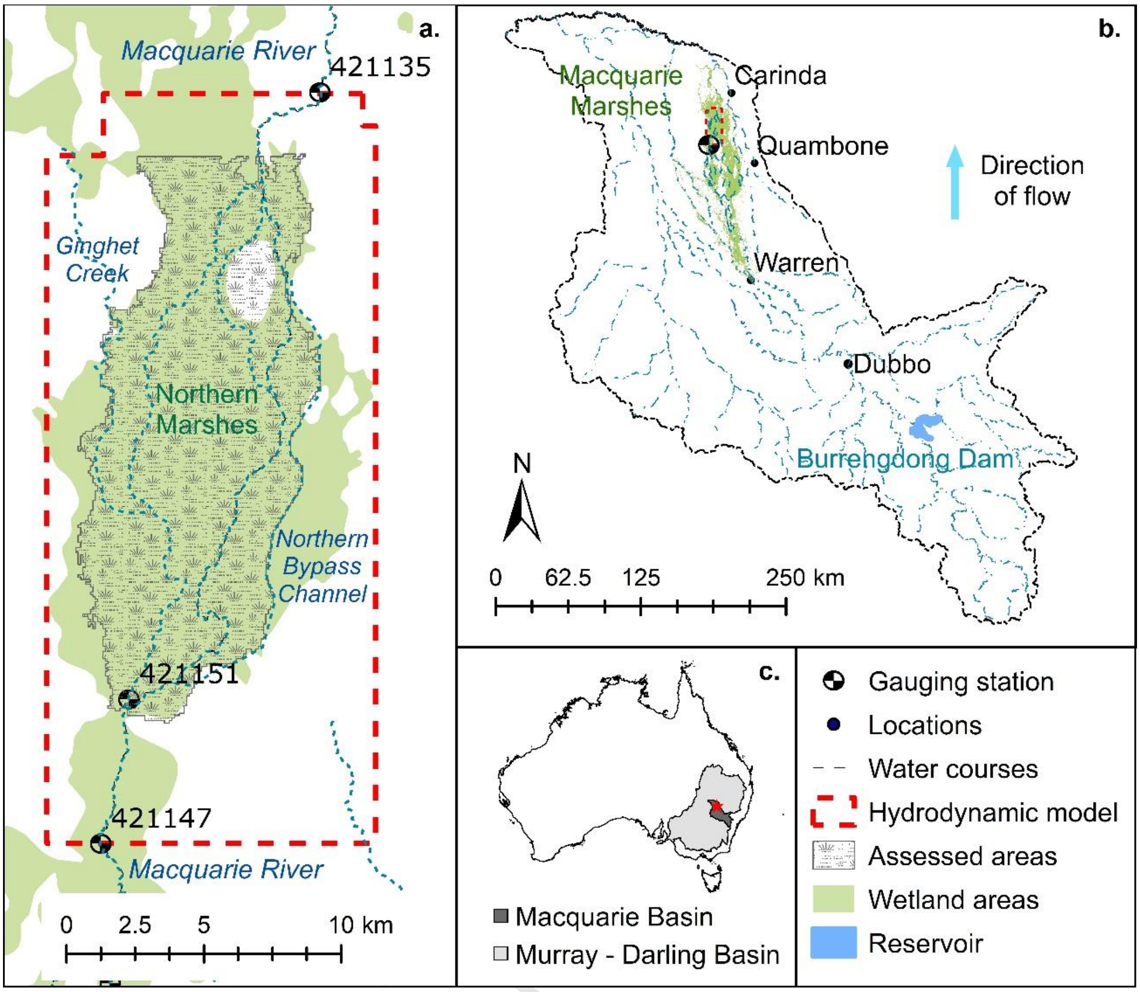

Figure 1. Characteristics of the study site. a) The Northern Marshes of the Macquarie Marshes and simulation domain, b) location of the Macquarie Marshes within in the lowland floodplain of the Macquarie River, c) location of Macquarie Basin within the Murray-Darling Basin in eastern Australia.

2.1. Hydrodynamic modelling

The water regime (i.e. inundation depth, duration and frequency) is determined from detailed spatio-temporal simulations of inundation patterns using a two-dimensional hydrodynamic model (Riccardi, 2000), which has been successfully implemented for simulating inundation of riverine floodplains (Garcia et al., 2015, Stenta et al., 2017) and coastal wetlands (Rodríguez et al., 2017, Sandi et al., 2018). The hydrodynamic model has also been calibrated and tested for the study site (Sandi et al., 2019). The simulation domain has a cell size resolution of 90x90 m and it covers the entire Northern

Marshes (Figure 1a). The topography of the domain was obtained from resampling a 1 m resolution LiDAR Digital Elevation Model (DEM).

The cells within the model domain are classified as either river or floodplain cells. Each cell contains characteristics of rivers and floodplains, which include river cross-sections and Manning's roughness according to the type of vegetation (Supplementary Table 1). The model has a total of 40 096 cells, of which 724 river cells represent the streams. Using this cell classification, the hydrodynamic model solves different versions of the shallow flow differential equations for mass and momentum conservation that are selected depending on the type of flow exchange between cells. For example, full dynamic equations are used for exchanges between two river cells, but for exchanges between floodplain a simplified diffusive wave approximation is used because flows are slower and inertial effects can be neglected (Riccardi, 2000). Other formulations are used for representing flow exchanges at hydraulic structures such as weirs and culverts as presented in Riccardi (2000), Rodríguez et al. (2017), and Sandi et al. (2018).

Inflows are input in the model as daily water levels recorded in the Macquarie River at gauging station No.421147 (Figure 1a) and downstream boundary conditions are set to the level of water levels recorded at gauging station No.421135 (Figure 1a) and projected over the floodplain. Water level data was obtained from WaterNSW (https://realtimedata.waternsw.com.au/). The calibration and model testing consisted of obtaining the best set of parameters that best-predicted water depths at station No.421151 (Figure 1a) and inundation extent when compared to satellite-derived inundation maps (Thomas et al., 2011) for flood events of different magnitudes. Calibration results and model testing showed excellent model performance for different events (Supplementary Figures 1,2 and Supplementary Table 2).

2.2. Vegetation dynamics modelling

The vegetation modelling approach uses results from the hydrodynamic model to describe the water regime in each cell in terms of three descriptors: duration of inundation, range of water depth and inundation frequency. The hydrodynamic simulations provide daily water depths at each grid-cell across the wetland, but changes in vegetation take place over longer timescales; therefore, we combined different descriptors over time by generating water depth vs. percentage exceedance time curves for each year of simulation. This allows integrating water depth and inundation duration. The frequency of inundation is assessed by comparing these curves over a sequence of simulated years of flow. Descriptors of the water regime are then integrated with vegetation-specific response functions to estimate vegetation transitions. These functions consist of inundation thresholds that represent the physiological water requirements of the vegetation. Transitions occur when the water regime is above or below the thresholds for the required frequency. Thresholds are derived from an assessment of the vegetation condition from ground surveys and vegetation maps (Bowen et al., 2017), Seasonal Fractional cover maps derived from Landsat 5 TM, Landsat 7 ETM+ and Landsat 8 OLI (JRSRP, 2014), and theoretical water requirements of each vegetation association (Roberts and Marston, 2011). A summary of these thresholds is presented in Table 1. Ground vegetation surveys and vegetation maps of the study site are available for the years 1991, 2008 and 2013 (Bowen et al., 2017). The first survey from 1991 was obtained after a series of years with large inundations so the vegetation map of that year provides a reliable description of the wetland system under wet conditions. The second survey from 2008 was obtained during the Millennium Drought when significant areas of the wetland had deteriorated so the vegetation map of that year provides a good description of the wetland areas under dry conditions. Finally, the third survey from 2013 was obtained after the break of the drought and after a series of record breaking rainfall events that produced significant recovery of the vegetation.

Table 1. Water regime requirements for different plant associations in the Macquarie Marshes.

Plant Association	Duration (%)*	Depth of water (m)	Frequency
Common reed (non-woody)	30% to 90%	0.02 to 0.5	1 in 3 years
Mixed marsh/ Water Couch (non-woody)	25% to 67%	0.02 to 0.6	1 in 3 years
River red gum (woody)	25% to 50%	0.02 to 0.6	1 in 5 years 1 in 7 years

Note: Adapted from Sandi et al. (2019), based on Roberts and Marston (2011). * Duration is presented as a percentage of the time inundated in a year.

The vegetation dynamics model is based on a series of rules that determine how the vegetation changes after each simulation step (one year). Decision treemaps illustrating and summarizing these rules are presented in Supplementary Figures 3 and 4. We assume that if the non-woody vegetation experiences no inundation or if the flood event is below the minimum for a series of years longer than the required frequency, the vegetation state will shift to a deteriorated state with potential encroachment from terrestrial vegetation. We also assume that terrestrial vegetation will transition back to non-woody vegetation after a year during which the inundation meets the physiological requirements of the non-woody vegetation (above threshold). This assumption is based on observations of rapid recovery of the non-woody vegetation after floods (Thomas et al., 2010, Bowen et al., 2017), which can result from different vegetation colonization mechanisms such as seed dispersal, seed banks and rhizome banks (Capon and Reid, 2016). It has been observed that Common reed can dominate patches of other non-woody vegetation associations (Bowen et al., 2017), so competition between non-woody vegetation is considered by assigning Common reed as the dominant vegetation association over Mixed marsh and Water Couch in cases where the water regime meets the physiological requirements for more than one association.

In the case of woody vegetation, we assume that if trees experience one above-threshold inundation in three years, conditions are good (0% - 40% apparent mortality). Vegetation will shift from good to intermediate conditions (40% - 80% apparent mortality) if the vegetation experiences no inundation or if the inundation is below the minimum from three to six consecutive years. Similarly, if the vegetation experiences no inundation or if the inundation is below the minimum for up to seven consecutive years the vegetation will shift to poor conditions (more than 80% apparent mortality). These assumptions are made based on observations of the vegetation dynamics on the site (Bowen et al., 2017), analysis of the vegetation response to inundation in the Macquarie Marshes (Sandi et al., 2019), and other studies of water requirements for River red gum (Doody et al., 2015).

We applied this same set of rules to the two models that have different spatial discretisation: a cellular automata model with rules applied to every individual cell, and a patch model with rules applied to entire patches of homogeneous vegetation associations. We assess the performance of both models by comparing the magnitude of the simulated vegetation extent over the entire domain against observed vegetation distribution (Bowen et al., 2017). Spatial data processing, calculations and visualization of results were carried out using ArcMap tools and MATLAB routines.

2.2.1 Cellular automata model

The first simulation approach consisted of setting up a simplistic cellular automata where changes in vegetation were tracked in each individual cell according to the inundation regime description. The resolution of this model was set to be the same as the hydrodynamic model (i.e. 90x90 m). Initial conditions were set the same as the vegetation state observed in 1991, and changes in each cell are defined by the water regime as a global driver using the threshold functions previously described.

2.2.2 Patch model

The second approach consisted of subdividing the simulation domain into patches of homogeneous vegetation associations. We converted vegetation distribution maps from polygons into raster files with the same resolution as the hydrodynamic model domain (90x90 m). We then used the patch vegetation distribution mapped in 1991 (wet conditions) and 2008 (dry conditions) (Bowen et al., 2017) to define 110 patches that could capture the observed flood-drought vegetation dynamics based on the observed vegetation and considering spatial features that could potentially affect vegetation response. For example, we subdivided large patches into riparian and floodplain patches as they may behave differently under future conditions, thus considering the proximity to streams. We also considered the topography and surrounding vegetation associations. Small patches (less than 20 cells) or small groups of overlapping cells that resulted from the conversion from polygon to raster were merged with larger patches that had similar dynamics. This was done in order to reduce bias in the estimation of patch integrated inundation values from the hydrodynamic model. The final patch distribution comprised patch sizes ranging from 0.16 km^2 (20 cells of the hydrodynamic model) to 6.8 km^2 (or 840 cells of the hydrodynamic model). This wide range of patch sizes is consistent with values reported for other wetland systems (Foti et al., 2013).

The assessment of the water regime is assessed within each patch by calculating the Minimum Inundation Index (MII) for each patch (Sandi et al., 2019), which consists of calculating the proportion of cells within each patch that satisfies the water regime requirements for a year of simulation (Table 1). By comparing the MII with the remotely sensed green vegetation fraction of the patch (JRSRP, 2014) and vegetation surveys (Bowen et al., 2017) on selected patches, we are able to identify the values of MII that result in healthy or deteriorated vegetation, and the threshold values that trigger transitions to other vegetation classes (Table 2).

Table 2. Range of MII thresholds.

Vegetation	Teste range of MII (% Area)	Calibrated value of MII (% Area)
Common Reed	10 – 65	50
Mixed Marsh/Water Couch	10 – 25	15
River Red Gum	10 – 60	55

Note: Sandi et al. (2019) reported the lower value of 10% for all vegetation associations. We have tested a larger range of thresholds for our simulations. Calibrated values are shown in the table.

3. Results

We carry out simulations of the vegetation dynamics over a period of 22 years (1991 to 2013) using both the patch and the cellular automata approaches. The patch model shows a much better performance than the cellular model in terms of the vegetation extent (Table 3). The highest differences between observed and simulated non-woody wetland areas are 2.6 km^2 in the patch model and 11.1 km^2 in the cellular model. The patch model produces relative errors below 5% for non-woody vegetation in 2008, but over predicts the extent of Mixed marsh and under predicts the extent of terrestrial vegetation in 2013. The cellular automata model produces relative errors higher than 10% for Common reed and higher than 80% for Mixed marsh in 2008 and 2013. The results of the patch model show a better response than the cellular model in terms of absolute errors, similarly to the non-woody vegetation results. For woody vegetation, the largest errors were obtained with the cellular automata model in both 2008 and 2013 where the highest differences in woody vegetation extent are 7.7 km^2 and 11.0 km^2 for 2008 and 2013 respectively. In the patch model, the highest differences in woody vegetation extent are 5.9 km^2 and 2.0 km^2 for 2008 and 2013 respectively. Although the woody vegetation extent errors are similar in magnitude to the errors for non-woody vegetation, errors for woody vegetation using the patch model are relatively smaller when compared to the total extent of woody vegetation (77.6 km^2).

Table 3. Total errors of simulated vegetation extent in 2008 and 2013 using the cellular automata and patch models.

Non-woody vegetation						
Year	Cellular automata			Patch model		
	Terrestrial vegetation	Common reed	Mixed marsh	Terrestrial vegetation	Common reed	Mixed marsh
2008	-6.1	-2.5	8.6	-0.9	0.7	0.2
2013	-5.2	-5.8	11.1	1.5	1.1	-2.6
Woody vegetation						
Year	Cellular automata			Patch model		
	Good	Intermediate	Poor	Good	Intermediate	Poor
2008	-4.9	-2.8	7.7	-5.9	0.1	5.8
2013	9.1	1.8	-11.0	-2.0	1.8	0.2

Note: All values are in km^2. Negative values indicate the model overestimates the vegetation extent.

During the drought, in 2008, the simulated spatial distribution of non-woody vegetation using the patch model (Figure 2a) shows a very good comparison to the observed vegetation (Figure 2b). Simulations using this model are able to reproduce a great deal of the terrestrial vegetation encroachment, denoting deteriorated wetland areas. In addition, the general distribution of Common reed and Mixed marsh/Water couch are simulated adequately during the drought period. In the cellular model (Figure 2c), the vegetation shifts towards an irregular pattern. Areas simulated as deteriorated and with terrestrial vegetation, encroachment show localized cell groups or single cells (Figure 2c) instead of homogenously deteriorated patches (Figure 2b). A complete loss of Mixed marsh is simulated with the cellular model, as Mixed marsh is either dominated by Common reed or encroached by terrestrial vegetation. The patch model is able to simulate patches of Mixed marsh remaining in 2008 and that later recovered in 2013. Both models adequately simulate the general spatial recovery of Common reed in 2013 (Figure 3a,b,c), however, in the cellular model the majority of recovered areas are dominated solely by Common reed and some areas show irregular patterns with small groups of cells that show no recovery (Figure 3c).

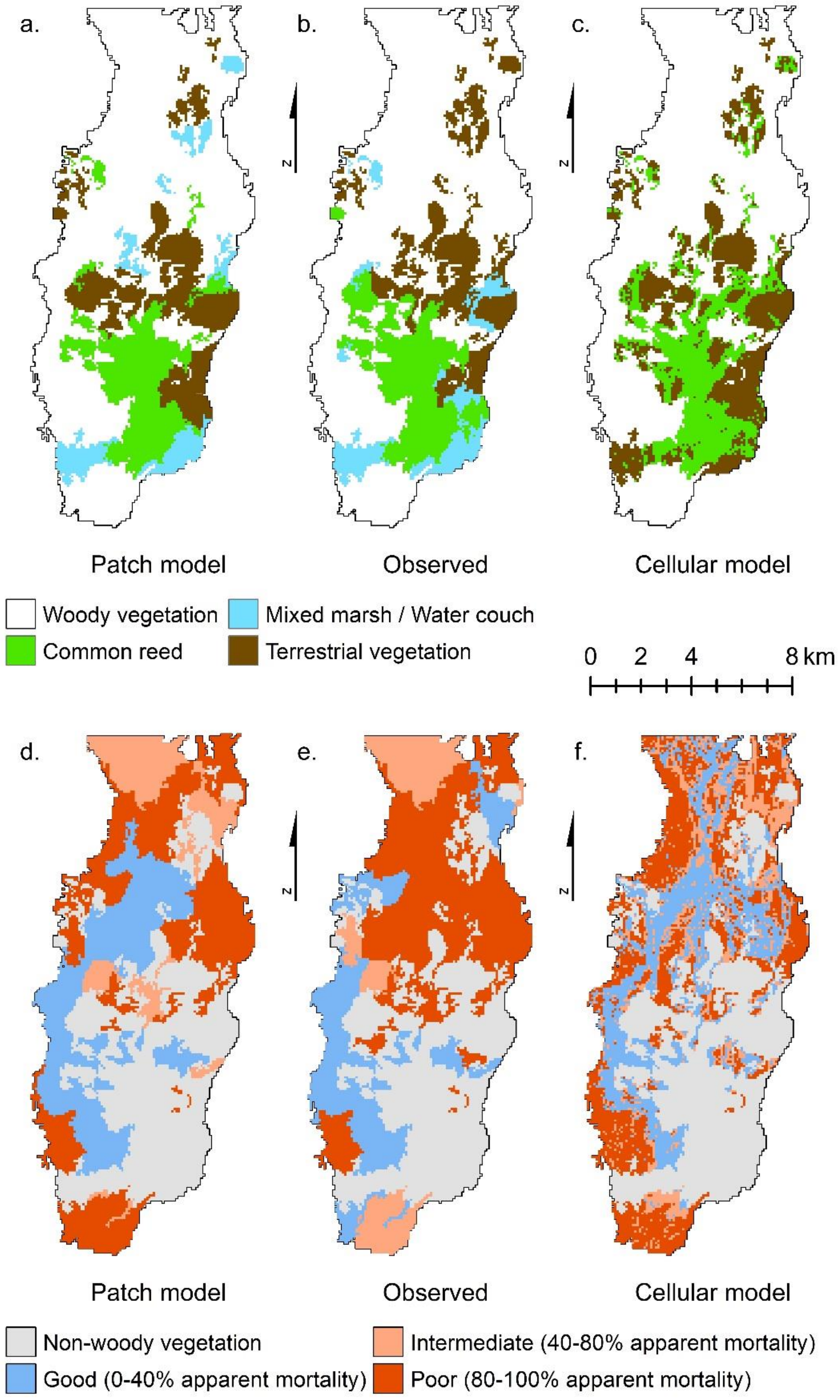

Figure 2. Comparison of observed vegetation in 2008 and simulated vegetation using a patch model and cellular automata. a, b, c) patch simulation, observed and cellular automata simulation of non-woody vegetation distribution. d, e f) patch simulation, observed and cellular automata simulation of woody vegetation condition.

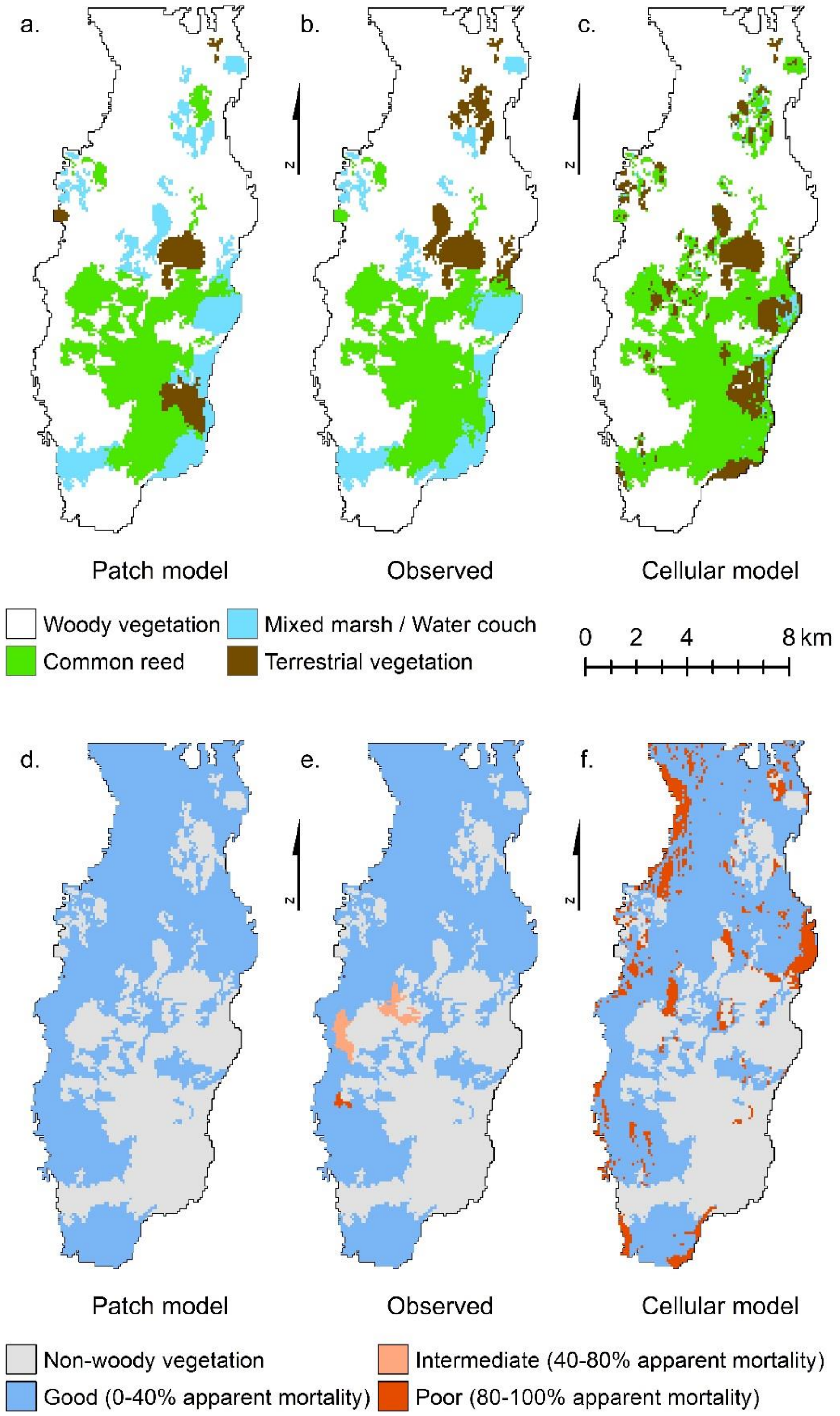

Figure 3. Comparison of observed vegetation in 2013 and simulated vegetation using a patch model and cellular automata. a, b, c) patch simulation, observed and cellular automata simulation of non-woody vegetation distribution. d, e f) patch simulation, observed and cellular automata simulation of woody vegetation condition.

Simulation of the woody vegetation condition using the patch model (Figure 2d) shows a good match in comparison to the observed conditions during the drought (Figure 2e). The largest mismatch occurs in the northernmost areas where the model overestimates some areas of trees in good condition and in the southernmost areas where the model shows some poor condition patches that were reported as intermediate and good condition. Simulation of the woody vegetation conditions in 2013 shows recovery in all woody vegetation with the patch model (Figure 3d), with very few mismatches when compared to the observed woody vegetation condition (Figure 3e). The cellular automata model shows a fair representation of the woody vegetation good condition in the southern parts of the wetland during drought, but it overestimates the extent of good woody vegetation condition in the northern areas (Figure 2f). In the cellular automata, cells in good condition are distributed around main water courses and there are also many small groups of cells isolated in the floodplain; cells representing the intermediate condition woody vegetation show irregular patterns surrounding the good condition areas. The cells in poor conditions during the drought that did not recover in 2013 are concentrated at the edges of the wetland, where the model classifies the vegetation as poor condition and grossly underestimates the recovery of the vegetation (Figure 2f and 3f). This occurs because the cells at the edges of the wetland are located further from the main streams and higher in the topography so the inundation simulated in those individual cells is not enough to produce a recovery of the vegetation.

Changes in the vegetation extent and condition show similar overall dynamics using both approaches, but with very distinct trends. Results from the cellular model show rapid changes in wetland vegetation extent even before the drought, while the changes from the patch model show vegetation being able to stay in stable states for longer periods of time. Cellular model simulations of non-woody vegetation show an increase in areas of terrestrial vegetation early in the simulation, even before the drought (Figure 4a), representing higher deterioration of non-woody wetland vegetation than simulations with the patch model. The majority of this higher deterioration obtained with the cellular model corresponds to Mixed marsh loss during most of the simulation period (Figure 4c). Mixed marsh loss is also a product of Common reed dominance as seen in the simulated 2008 and 2013 vegetation extent maps (Figure 2c, 3c), therefore, Common reed shows higher extent in the cellular model than the patch model (Figure 4b). The cellular automata model shows a more rapid deterioration of the condition of woody vegetation with a decrease in the extent of good condition woody vegetation in the 1990's (Figure 4d), a gradual decrease in the 2000's during the drought period and recovery at the end of the simulation. In contrast, the patch model shows that almost all patches of woody vegetation stay in good conditions up until the drought period, during which there is a 64% decrease of areas in good conditions with full recovery after the break of the drought at the end of the simulation (Figure 4d). The behaviour of the intermediate and poor condition woody vegetation is also quite different between the patch model and the cellular model. The more rapid deterioration of woody vegetation modelled with the cellular model results in areas with intermediate conditions early in the simulation (Figure 4e) that reach poor conditions before the drought period (Figure 4f). In addition, the cellular model also shows significantly less recovery at the end of the simulation in comparison to the observed vegetation and the patch model results.

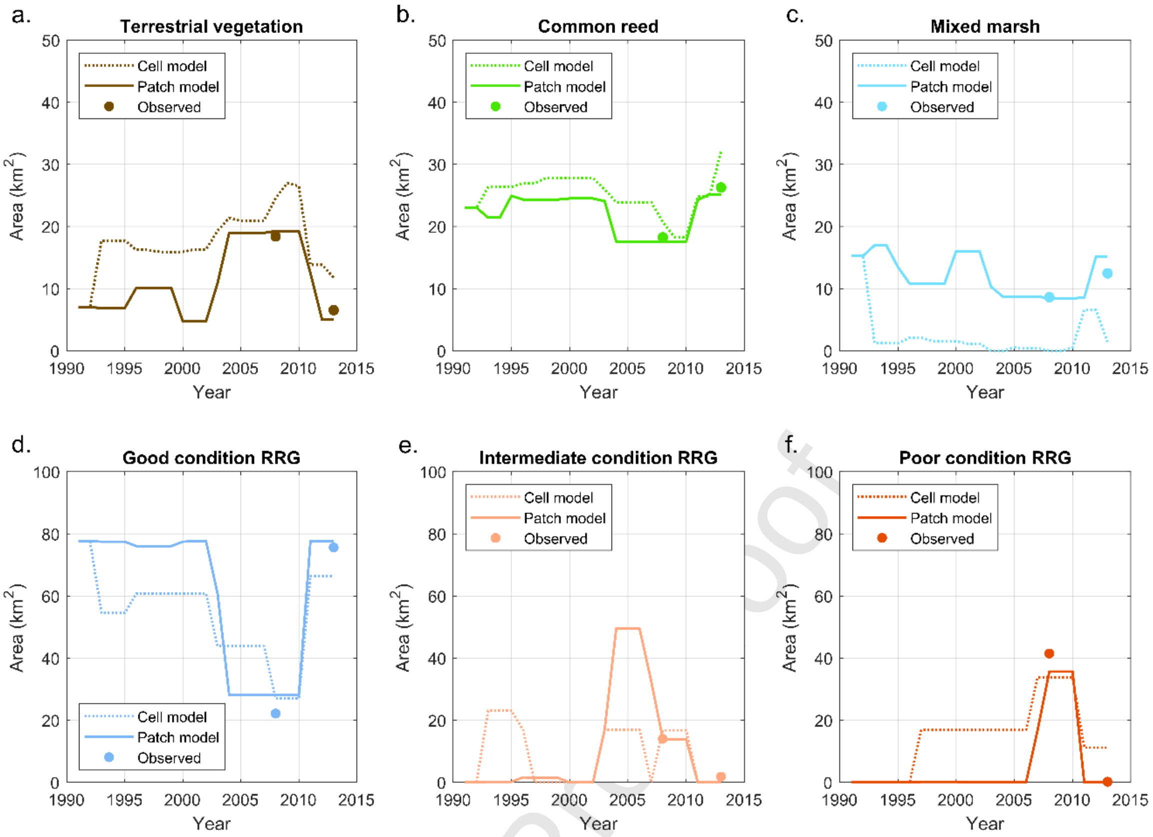

Figure 4. Non-woody vegetation extent and woody vegetation condition time series between 1991 and 2013. a) Terrestrial vegetation. b) Common reed. c) Mixed marsh. d) Good condition River red gum. e) Intermediate condition River red gum. f) Poor condition River red gum. Note: Observed vegetation in 2008 and 2013 are used to estimate errors in the simulation.

The combined extent of areas of poor woody vegetation conditions and non-woody vegetation that transitioned to terrestrial vegetation shows that the cellular model severely overestimates the impacts of drought on the wetland system (Figure 5a). Results show that after 3 years of simulation, non-woody vegetation starts to experience deterioration in the cellular model, and after 7 years of simulation, conditions of woody vegetation reach poor conditions which produce a significant increase in the total deteriorated area (Figure 4 and Figure 5a). Unlike the patch model, after the large floods experienced in 2000, the cellular model is not simulating a recovery of the vegetation. Deteriorated conditions reach a peak in both models during the drought period, coinciding with the observed conditions in 2008. The median deteriorated extent simulated with the cellular model is 33.1 km^2 with a much larger spread of values than the patch model with a median of 10.3 km^2 (Figure 5b). In the patch model, the severely deteriorated conditions of the vegetation during the drought are extreme values that are maintained only during the last years of the drought, whereas in the cellular model deteriorated conditions are perceived to a larger extent for a longer period of time.

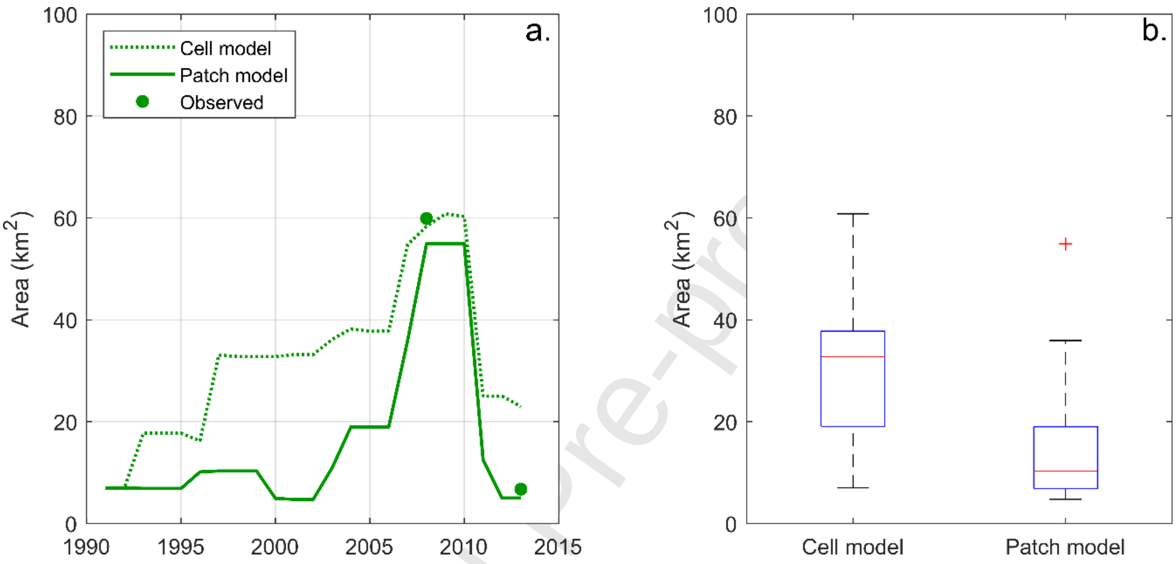

Figure 5. a) Simulated extent of deteriorated wetland or terrestrial encroachment time series between 1991 and 2013. b) Range of deteriorated wetland extent. Note: Observed vegetation in 2008 and 2013 are presented in a) for comparison. Red line in b) represents the median, the lower and upper values of the box represent the 25th and 75th percentiles respectively, whiskers represent the extent of the most extreme data, and data represented with + are considered outliers.

4. Discussion

We have developed a cellular automata model and a patch model for simulating the vegetation dynamics of dryland wetland systems and we have applied the models to a wetland site in semiarid Australia. Both models are able to simulate vegetation deterioration during drought periods and recovery after the drought break, correctly representing the adaptability of the vegetation. Vegetation in dryland regions is able to adapt between stable states, which are conditioned by the water regime during wet and dry periods (Colloff and Baldwin, 2010). This adaptability follows a complex cycle in which vegetation varies responding to the water regime, which is one of the main global drivers of vegetation adaptability cycles in dryland wetlands. Productivity increases during wet periods until a maximum is reached, then there is a decrease in productivity when floods start to recede and minimum productivity is reached during dry periods (Thapa et al., 2016). When dry periods exceed the capabilities of the vegetation to adapt, transitions to dryer states are prone to occur and the vegetation will transition to terrestrial vegetation which is capable of surviving under very limited water availability. Transitioned vegetation is also able to return to a previous stable state of wetland under the adequate conditions determined by global and local drivers because adaptability cycles also work between stable states and between different scales of an ecosystem (Thoms et al., 2018). Overall, the water regime acts as an overarching global driver over the wetland domain, which defines the conditions for different stable states to establish. Local drivers act as "memory" functions, which allow the vegetation to recover or regenerate after transitions have occurred.

The results of the simulated vegetation dynamics in dryland wetlands demonstrate that both models are a good representation of adaptability cycles and the transition between stable states, but the patch model has shown a much better performance than the cellular model simulating the general spatial distribution of the vegetation (Figure 2, 3), the total vegetation extent (Figures 4, Table 3), and the vegetation condition (Figure 5). These results suggest that considering the water regime as a global driver, in combination with a patch discretization, provides a better representation of the vegetation dynamics. The reason for this might be that the patch discretization can indirectly represent the effects of local drivers. Despite operating at a small scale, local drivers act in spatially distributed patterns, which contribute to the underlying mechanisms for observed vegetation organization in small groups or patches of dominant species. The water regime has a strong influence on the composition of local drivers like seedbanks (Capon and Brock, 2006, Pueyo et al., 2008). In general, seeds are more abundant in more frequently inundated areas. This helps to promote the establishment of patch like distributions and regeneration of frequently inundated areas. In less frequently inundated areas, wetland vegetation is deteriorated during a drought, but regeneration might be limited due to seedbank availability. Vegetation does not solely rely on local seedbanks for regeneration, they can also survive in situ through persistent rhizomes and shoots (Capon and Reid, 2016). In these cases, initial states of the vegetation and persistence of rhizomes banks during the drought period would play a crucial role in the vegetation resilience and spatial organization. The non-woody vegetation associations in the study site have the capability of regenerating from both seedbanks and rhizome banks.

Other local drivers can also promote the organization of the vegetation. Woody vegetation species, such as River red gum, have root structures evolved to take advantage of the available water. During times of water deficit, trees access water deeper underground via the 'sinker roots' and during flood periods the trees can access water through a dense network of fine roots near the soil surface (Doody et al., 2015). Root networks extend beyond the shade of the canopy and their area of influence covers a significant extent within the patch (McGregor et al., 2016), which can promote other local drivers such as soil moisture redistribution (Foti and Ramírez, 2013), also influencing the organization of the vegetation in patch-like distributions. Additionally, surface mechanisms such as resource redistribution and connectivity (D'Odorico et al., 2007, Okin et al., 2015, Saco et al., 2018, Saco et al., 2020) and interspecies competition (Coletti et al., 2017) can also be related to the water regime and influence the organization of vegetation patterns.

In the cellular model, we have not included local drivers, as the inclusion of such drivers requires the definition of complex neighbourhood functions to represent specific processes occurring at a scale smaller than the cell size (Fonstad, 2006), which would require a higher level of detail and data for calibrating and validating the model. However, in our study, the water regime appears to act as a global driver over a scale larger than the cell size resolution. The observed dynamics and organization of the vegetation show groups of cells with homogenous vegetation states or a patch like distribution rather than the heterogeneous patterns simulated with the cellular model. The targeted phenomena in our simulations are the changes in vegetation (and vegetation state) extent. However, the patterns captured by the cellular model are heterogeneous and at a smaller scale, therefore, spatial averaging used in the patch model reduces the complexity of the model and improves the representability of the desired emerging processes (Larsen et al., 2016). Interestingly, it would be expected that the pre-definition of patches in the model would restrict the representability of the output as the change occurs in pre-defined groups of cells instead of cell by cell, but our simulations of the vegetation extent using both approaches (Figure 4) show similar vegetation dynamics. In both approaches, the extent of the vegetation has periods where the simulated extent is almost constant between significant transitions. The pre-definition of the patch requires detailed analysis and extensive information for delimiting the boundaries of the patch arrangement, but this approach is more convenient in cases of limited information as our results suggest that employing a patch discretization aids the representability of the model with a better performance and similar dynamics to a cellular automata.

In terms of representing deteriorated wetland areas, the cellular model shows higher deteriorated areas than the patch model. This is the result of some cells not receiving enough inundation, as they are located higher in the topography or near the edges of the simulation domain and the numerical solution of the hydrodynamic model shows very little inundation in these cells. In the site, areas further away from streams and main channels receive less water during flood periods, but vegetation surveys have identified that the patches near the edges of the wetland are able to maintain healthy condition or recover (Bowen et al., 2017). This suggests that the cellular model overestimates deteriorated areas and therefore significantly underestimates the resilience of the vegetations. The vegetation in the cells that do not fully inundate might still be benefiting from the inundation by local drivers like water and resources redistribution, which is indirectly captured in the patch model. This leads to the conclusion that the assessment of deteriorated areas using the patch model would be a more realistic representation of the mechanisms that control vegetation changes and the resilience of the vegetation under flood and drought cycles.

The methods and framework implemented using a patch distribution model shows great potential for simulating the dynamics of dryland wetlands under flood and drought periods. The development of such models requires relatively fewer data and information than a fully integrated cellular automata, therefore, such methods can potentially be extrapolated for the analysis of other dryland wetlands systems and used to explore the vegetation dynamics of the wetland under different scenarios of environmental water management and climate change. Our physically-based approach makes use of a spatially distributed hydrodynamic model in order to provide detailed descriptions of the flood and takes advantage of vegetation datasets that describe the state and the spatial distribution of the vegetation during wet and dry years. Limitations for developing such a model in other systems will depend on the availability of such information. For example, low-quality topographic data will limit the implementation of a hydrodynamic model, affecting the representation of the water regime, and limited information on vegetation distribution will complicate the definition of the vegetation response relations. In our model, we have integrated hydrodynamic simulations with available vegetation maps (Bowen et al., 2017) and readily available remote sensing products (JRSRP, 2014) to determine thresholds for vegetation transition using the methodology from Sandi et al. (2019). Continuous data collection and monitoring of the vegetation extent can be used to develop more detailed and complex relations between flow and vegetation that can improve model performance.

The spatial resolution is also an important aspect that needs to be taken into account. Ultimately, the spatial resolution used in any model will be a compromise between the desired level of detail and computational cost. However, it is essential that the spatial resolution is high enough so it can represent the desired processes. Our model domain has a total area of 224.8 km^2 with a resolution of 90x90 m, which represents an acceptable compromise in terms of the hydrodynamic simulations as the model has a good performance with an acceptable level of detail. In the absence of detailed information in terms of vegetation dynamics at our site, we have assumed that water regimes drive rapid transitions between vegetation states. In general, expansion of dominant species such as Common reed and Water couch may not always occur rapidly or at the spatial (i.e. 90m×90m or patches) resolution of the model due to other limiting factors like seed or rhizome availability. However, the seed banks in the ephemeral dryland wetlands of Australian floodplains are very diverse and abundant (Capon and Brock, 2006), as are rhizome and propagule banks. The rich and viable seed, rhizome and propagule banks respond rapidly to hydrological regimes (Reid et al. 2016) and support the ecological resilience in this type of landscape (Capon and Reid, 2016). Floods with sufficient depth and duration can promote regermination and growth of these non-woody species in a short period (months), replacing the existing terrestrial species that died off due to waterlogging. The general dynamics generated by these processes are adequately represented in the patch model for our particular study site. In the cellular automata model, these processes are not fully represented, as more data is required to generate neighbour rules to represent these processes.

5. Conclusions

Our results support the initial hypothesis of the study. By aggregating the analysis of vegetation dynamics in dryland wetlands using a finite patch distribution, the water regime provides an indirect representation of local drivers and an overall better performance simulating vegetation extent. Local drivers seem to provide significant control over the vegetation dynamics, but the inclusion of such drivers in a cellular automata model might require large amounts of information and data to derive transition functions that need to be calibrated and validated. The patch model setup proved to be a versatile tool to simulate vegetation dynamics and it might be a convenient approach in cases where data availability is limited. Future investigations of wetland vegetation resilience in other systems may benefit from such approach. The patch model approach, however, does require detailed analysis for initial patch delimitation. The results of this contribution suggest that the patch discretization provides a better representation of changes in the vegetation, which is of major importance for the assessment of wetland resilience under flood-drought periods.

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Credit Author Statement

S.G.S., J.F.R., P.M.S conceptualized the study. S.G.S. designed and conducted all experiments (with input from J.F.R., P.M.S. and G.R.). S.G.S., J.F.R. and P.M.S. wrote the paper with substantial input from N.S., L.W., G.K., G.R., and G.W. All authors contributed to interpretation of the results and revision of the manuscript.

Graphical abstract

Highlights

- Vegetation resilience studies in dryland wetlands need realistic modelling tools
- Vegetation dynamics are mainly influenced by the water regime as a global driver
- We compare a simplified cellular automata model and one with a patch discretization
- Patch discretization model performs better simulating wetland vegetation extent
- Patch model indirectly includes local drivers that influence vegetation dynamics

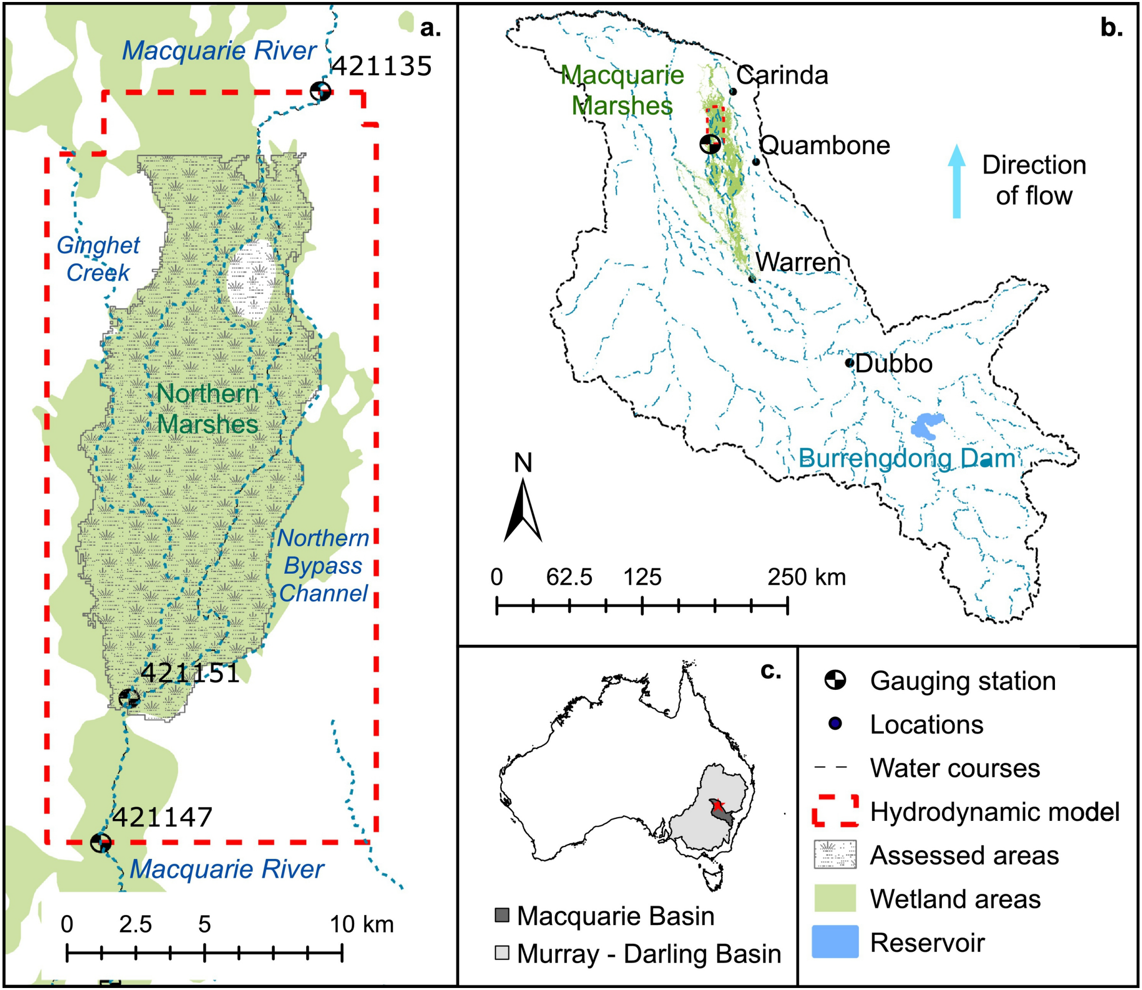

a.
Macquarie River
421135
Ginghet Creek
Northern Marshes
Northern Bypass Channel
421151
421147
Macquarie River
0
2.5
5
10 km
b.
Macquarie Marshes
Carinda
Quambone
Warren
Dubbo
Burrengdong Dam
Direction of flow
N
0
62.5
125
250 km
c.
Macquarie Basin
Murray - Darling Basin
Gauging station
Locations
Water courses
Hydrodynamic model
Assessed areas
Wetland areas
Reservoir

Figure 1

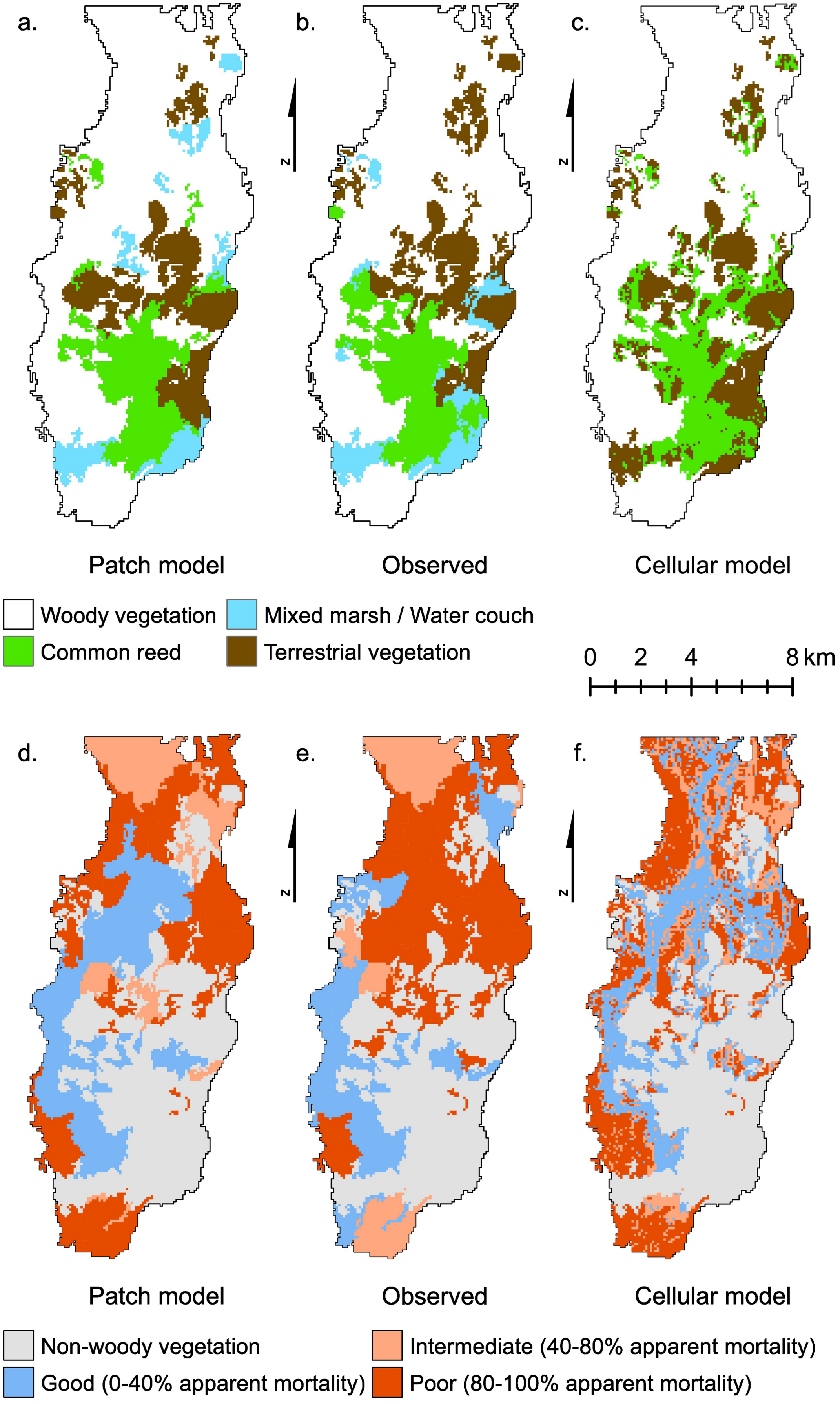

a.
b.
c.
N
N
Patch model
Observed
Cellular model
Woody vegetation
Mixed marsh / Water couch
Common reed
Terrestrial vegetation
0
2
4
8 km
d.
e.
f.
N
N
Patch model
Observed
Cellular model
Non-woody vegetation
Intermediate (40-80% apparent mortality)
Good (0-40% apparent mortality)
Poor (80-100% apparent mortality)

Figure 2

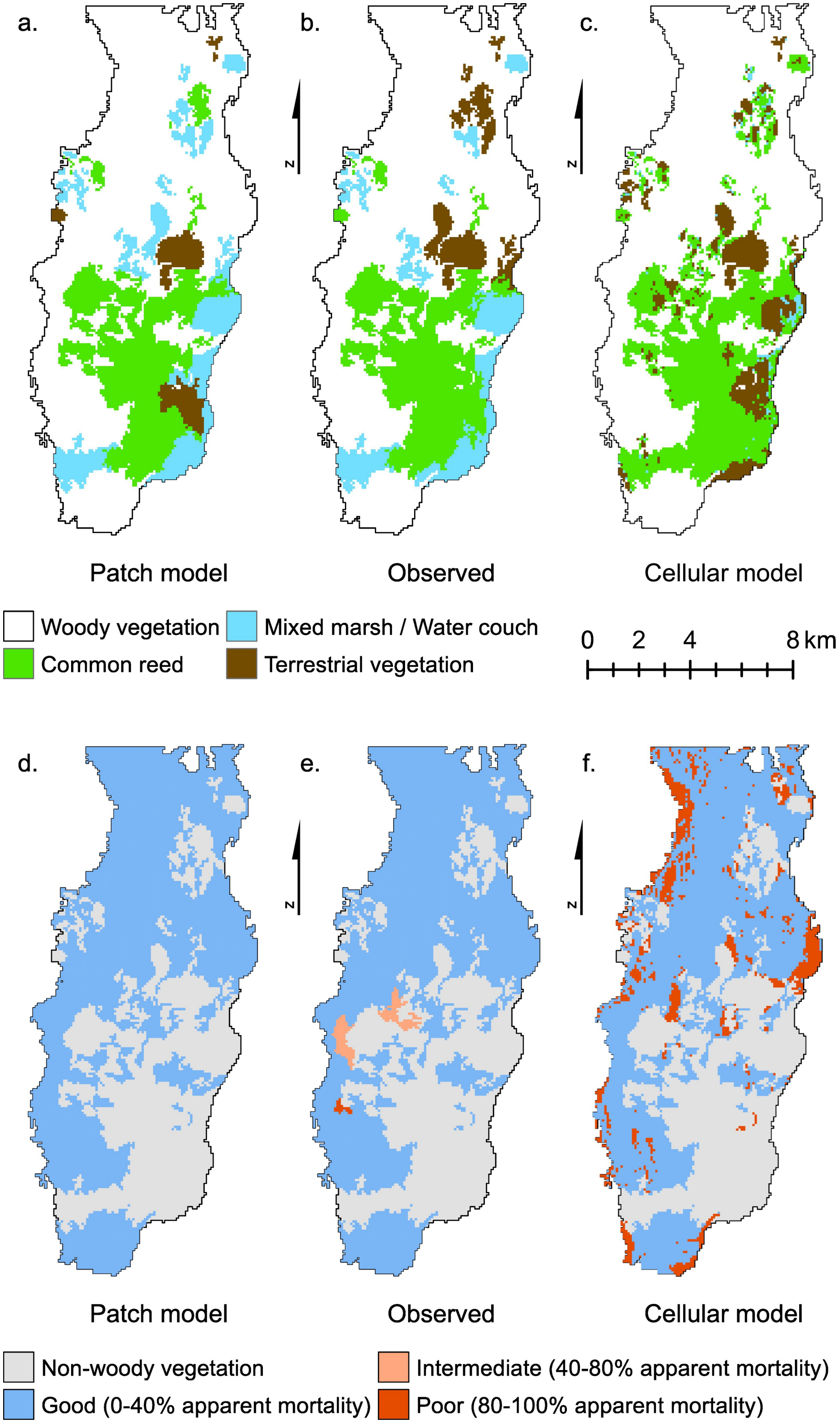

a.
b.
c.
N
Patch model
Observed
Cellular model
Woody vegetation
Mixed marsh / Water couch
Common reed
Terrestrial vegetation
0
2
4
8 km
d.
e.
f.
N
Patch model
Observed
Cellular model
Non-woody vegetation
Intermediate (40-80% apparent mortality)
Good (0-40% apparent mortality)
Poor (80-100% apparent mortality)

Figure 3

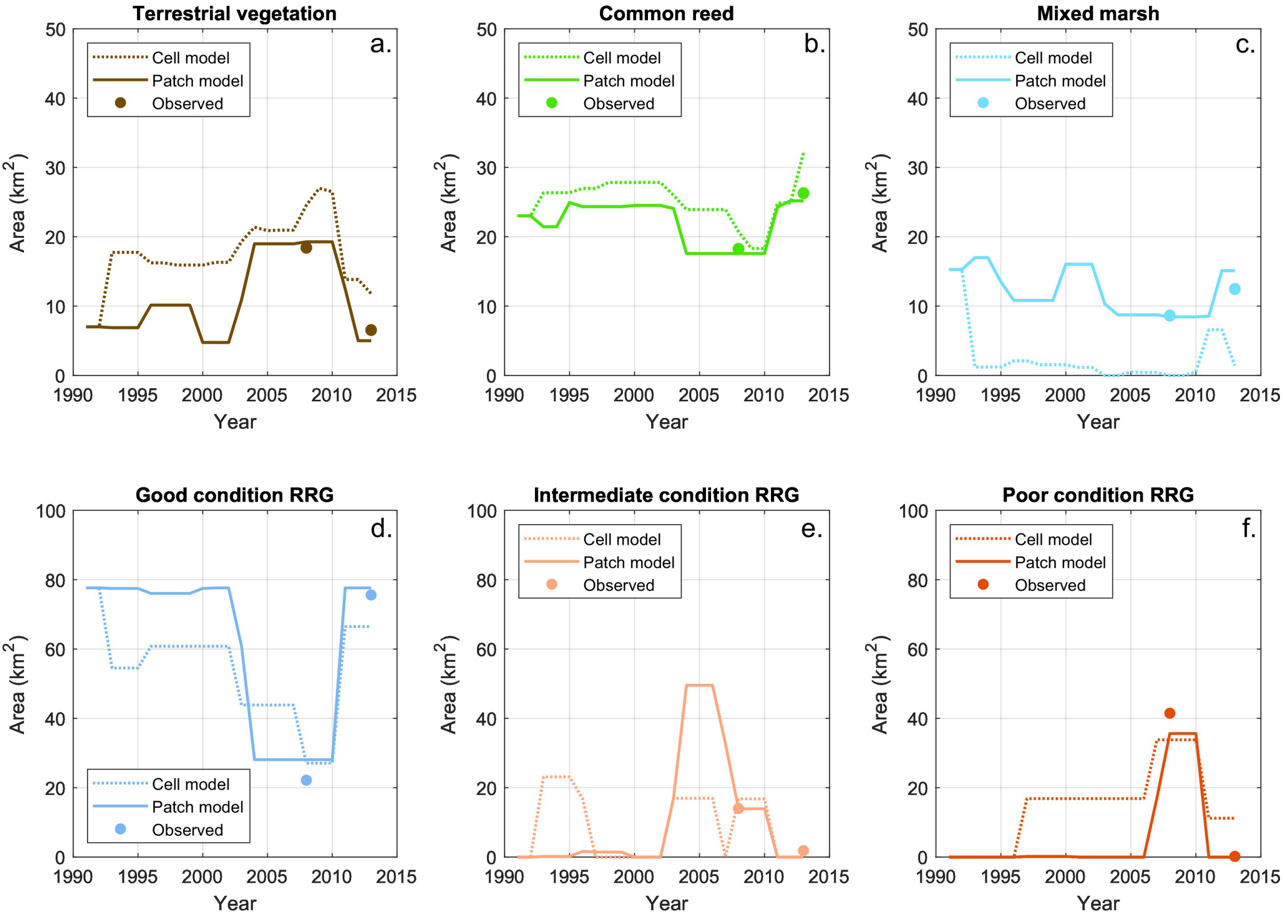
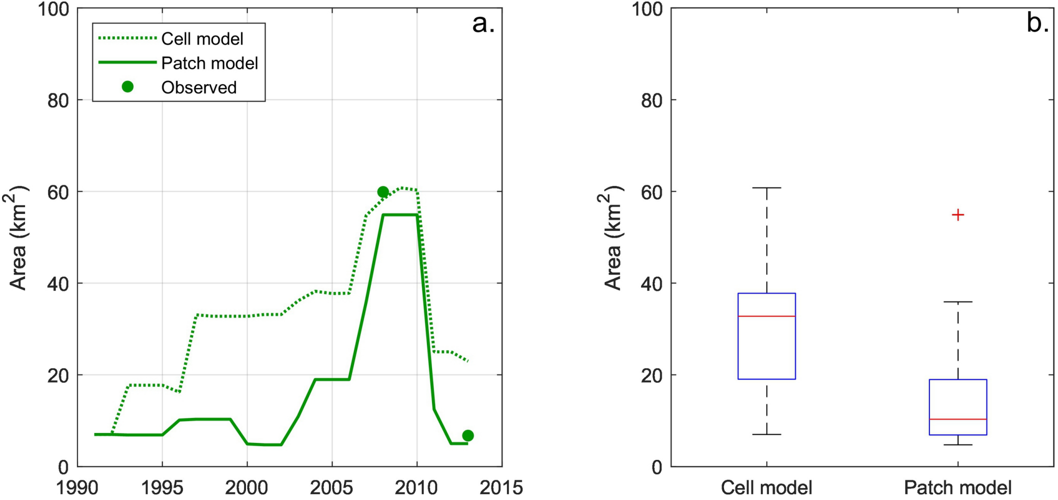

Terrestrial vegetation
Common reed
Mixed marsh
Good condition RRG
Intermediate condition RRG
Poor condition RRG
a.
b.
c.
d.
e.
f.
Cell model
Patch model
Observed
Area (km²)
Year
0
10
20
30
40
50
60
80
100
1990
1995
2000
2005
2010
2015

Figure 4



a.
b.
Cell model
Patch model
Observed
Area (km^2)
0
20
40
60
80
100
1990
1995
2000
2005
2010
2015
Cell model
Patch model

Figure 5