

Planning for reserve adequacy in dynamic landscapes; maximizing future representation of vegetation communities under flood disturbance in the Pantanal wetland

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ABSTRACT

Aim Using a probabilistic modelling framework, we aimed to incorporate landscape spatiotemporal dynamics into reserve design. We employed a spatially explicit stochastic model, which integrates both hydrological and biological processes, to simulate the wetland's biological succession.

Location Pantanal wetland (with 140,000 km²) between Brazil, Bolivia and Paraguay.

Methods We used the reserve design software Marxan to optimize the current and future representation (up to 50 years) of 20% of five plant communities with maximum reliability (i.e. smallest uncertainty). The Kappa statistic was used to compare selection frequencies of individual sites through a set of planning timeframes (5, 17, 25 and 50 years) and the likely pattern of biological succession over these periods.

Results Solutions based on static vegetation distributions were significantly dissimilar from solutions based on the expected modelled changes resulting from the flood disturbance and succession dynamics. Increasing the required reliability of biodiversity outcomes resulted in more expensive reserve solutions. We demonstrated the flexibility of probabilistic decision-making methods to illuminate the trade-offs between reliability and efficiency of site selection.

Main conclusions Considering the importance of habitat heterogeneity to the principles and practice of systematic conservation planning, it is notable that landscape dynamics have not been a central theme in conservation planning. In the case of the Pantanal hydrosere, acknowledging and planning for temporal dynamics required an ability to model succession and define acceptable levels of outcome reliability, but ultimately improved the long-term Adequacy of resulting reserve networks.

Keywords

Conservation planning, flood dynamics, Marxan, probabilistic model, succession, wetland.

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INTRODUCTION

Recent estimates suggest that half of Earth's wetland systems have already been destroyed (Zedler & Kercher, 2005). Agricultural and industrial demand for water is compromising further the quantity and quality of aquatic habitats all over the

globe (Mitsch, 2005a). Hence, flow reduction has become the major factor threatening wetlands (Klinge *et al.*, 1990; Gopal *et al.*, 2000). To protect such complex systems, we need to consider issues that go beyond the simple representation of species and habitats (typically used as the basis of conservation plans) – we need to consider ecosystem processes.

Understanding ecological process dynamics and functionality through time constitutes an increasingly central part of wetland conservation planning (Gibbs, 2000; Gopal *et al.*, 2000; CBD, 2004; RAMSAR, 2004).

Disturbance and subsequent biological succession are some of the driving forces that structure processes, species diversity and abundance in plant communities (Clements, 1916; Scanlan & Archer, 1991; Klinger, 1996; Amarasekare & Possingham, 2001; Mark & Wilson, 2005; Rammig *et al.*, 2006). Successional processes are often incorporated into management plans to restore wetland functionality (Lamb, 1998; Wan *et al.*, 2001; Ward *et al.*, 2001; Zedler & Kercher, 2005; Rammig *et al.*, 2006), however, are rarely considered in systematic conservation plans (Turner *et al.*, 1999; Mitsch, 2005b; Chan, 2006; Franklin, 2010).

Many models of successional dynamics in wetlands have used Markov chains to describe the stochastic processes behind community behaviour, because they use probabilistic methods to account for the likelihood of transition between seral stages. However, succession is dictated by the hydroperiodic signature of each wetland (i.e. the most frequent combination of flood intensity, frequency, extent and duration). Combined, such understanding allowed humans to develop management strategies and restoration plans for wetland ecosystems (Tutin, 1941; Van Hulst, 1979; Li, 1995; Klinger, 1996; Logofet *et al.*, 1997; Toner & Keddy, 1997; Wu *et al.*, 1997; Childress *et al.*, 1998; Balzter, 2000; Klein *et al.*, 2005). We used our knowledge of the Pantanal's hydroperiodic signature to develop a model that can help us predict the effect of floods on succession dynamics (Gopal *et al.*, 2000).

The spatial distribution of wetland communities, present in a dynamic equilibrium state, is largely determined by the life history traits of their constituents (Connell & Slatyer, 1977). This effect called *systems' memory* and defined by how long the past influences the future state of the system can vary from just a few years in aquatic hydrosere (Walker, 1970) to hundreds of years in forest succession (Hall *et al.*, 1991). These forces are considered to be responsible for the patchy structure of wetlands and have been described using Markovian models (Johst & Huth, 2005). This is because, under the influence of biogeographical forces and temporal stochasticity (DeAngelis *et al.*, 1998; Johnson, 2004), these systems have a propensity to reach stable distribution, where several habitats or seral stages can coexist (Burgman *et al.*, 1992).

In recent years, disturbance models have been considered in systematic reserve selection to incorporate the effect of catastrophic events such as fires, hurricanes and coral bleaching, and their impact on biodiversity and on the success of protected areas (Platt & Connell, 2003; Keane *et al.*, 2004; Leroux *et al.*, 2007a; Game *et al.*, 2008). While catastrophes can cause massive jumps in biological succession (e.g. hurricanes destroying old growth forest and coral reefs), flood disturbances in wetlands are less dramatic, their effects are bidirectional considering that the absence of floods also result in successional changes (Richards *et al.*, 1999; Johst & Drechsler, 2003; Leroux *et al.*, 2007b; Drechsler *et al.*, 2009). In the case

of the flood/drought cycle, seral stages can be independently pushed back and forward along the terrestrialization-paludification gradient instead of jumping unidirectionally to the earliest stage of succession (Junk, 1989; Mitsch & Gosselink, 1993; Klinger, 1996).

Several studies have tried to incorporate the probabilistic occurrence of species and communities into systematic conservation planning decisions (Margules & Nicholls, 1987; Polasky *et al.*, 2000; Cabeza *et al.*, 2004; Sakar *et al.*, 2004; Nicholson & Possingham, 2006; Game *et al.*, 2008; Becker *et al.*, 2010; Carroll *et al.*, 2010). For stochastic systems, the use of a probabilistic framework provides predictive models with a natural currency that can help explicitly define the uncertainty around solutions (Sakar *et al.*, 2004). Markov chains are considered particularly helpful in predicting future states of systems that rely on past transitional conditions (Balzter, 2000; Polasky & Solow, 2001; Cabeza *et al.*, 2004; Wilson *et al.*, 2005). However, coupling of flood and vegetation models under temporal stochasticity for the purpose of designing representative and adequate reserve systems is still a frontier in systematic conservation planning (Kiester *et al.*, 1996; Margules & Pressey, 2000; Arthur *et al.*, 2002; Leroux *et al.*, 2007b).

METHODS

The study region

The Pantanal is the biggest contiguous freshwater wetland ecosystem in the world (Mittermeier *et al.*, 2005). Nested in the Upper Paraguay River basin (365,000 km²), the floodplain is shared by Brazil, Bolivia and Paraguay, with, c. 70% (140,000 km²) of the wetland ecosystem lying within Brazilian territory (Fig. 1). Like the floodplains of central Amazon, the Pantanal has been characterized as a pulsing system with markedly wet and dry phases (Junk, 1992; Junk & da Silva, 1999). The temporal dynamics of flood disturbances are a recognized driver of the Pantanal biodiversity's spatial heterogeneity, and environmental services (Ab'Saber 1988; Assine & Soares, 2004; Harris *et al.* 2005; Junk & Nunes da Cunha, 2005).

The Pantanal floodplains are among most biodiverse wetlands in the world (Zedler & Kercher, 2005), with healthy populations of threatened species such as Hyacinth macaws (*Anodorhynchus hyacinthinus*), marsh deer (*Blastocerus dichotomus*), giant river otters (*Pteronura brasiliensis*) and jaguars (*Panthera onca palustris*). These species are particularly dependent on the wet and dry phases of the ecosystem for water, food and shelter (Crawshaw & Quigley, 1991; Quigley & Crawshaw, 1992; Mourão & Campos, 1995; Rosas *et al.*, 1999; Guedes, 2004; Fonseca *et al.*, 2005).

In recent years, human activities have become a major force in shaping the ecology of the Pantanal. Deforestation, river damming and wildfires are disrupting plant community dynamics (Padovani *et al.*, 2004; Junk & Nunes da Cunha, 2005). Such interventions may compromise ecosystem func-

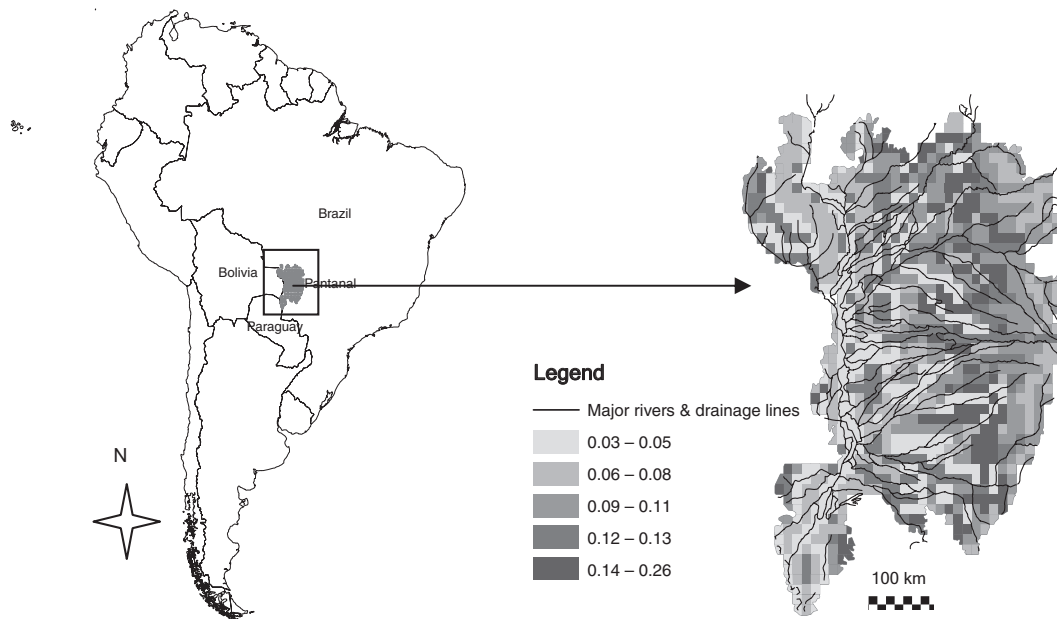


Figure 1 Map of South America and its country borders with an insert showing the Pantanal flood probability map (1:100,000). The grey scale provides the flood probabilities over the last century for each site, which was interpolated from Hamilton's (1996) model as the probability of flooding of site i , based on topography and distance from rivers.

tions and jeopardize environmental services estimated at US\$ 15.5 billion (Seidl & Moraes, 2000).

Despite its economic importance and the abundance of rare and threatened species, recent reviews showed severe shortcomings in the protected areas system for the Pantanal (Rylands & Brandon, 2005), with < 5% of its surface covered by public and private reserves. Even the expansions of priority areas proposed for the Brazilian Pantanal (Ministério do Meio Ambiente, 2007) failed to deliver on two of the four basic principles of conservation planning, representation and efficiency (Possingham *et al.*, 2006; Lourival *et al.*, 2009).

Wetland dynamics and conservation

The aim of this paper is to develop an ecologically relevant picture of conservation needs in the Pantanal, by incorporating hydrological disturbance and ensuing successional ecosystem dynamics into systematic conservation. We present a conservation planning method that can better deliver on the conservation principle of adequacy, whereby the resulting reserve systems presumably superior in their long-term conservation performance (Possingham *et al.*, 2006). We illustrate our study with an example of the Pantanal wetland in South America (Por, 1995; Mittermeier *et al.*, 2005; Drechsler *et al.*, 2009). Our objective is to select a set of sites which represents 20% of the occurrences of vegetation succession stages, while also maximizing the chance of retaining such targets 50 years into the future, because they are assumed to represent the breadth of regional biodiversity. We implement our approach with the decision support system Marxan (Ball & Possingham, 2000; Game *et al.*, 2008) and

compare the reserve selection outcomes (variance of site selection frequency scores) under static and dynamic conditions.

Vegetation classification

Because we were interested in successional stage dynamics, we clustered the 17 vegetation classes of Da Silva *et al.* (2000), into five functional clusters. We added a fifth class to Naiman's classification system to account for a climax seral stage, which in the Pantanal represents the influence of upland mesic vegetation occurring in higher topographic regions of the floodplain (Naiman & Decamps, 1997). These clusters represent a set of recognizable successional stages distributed in 1126 grid cells, each of about 10,000 ha, defined as our individual planning units, mapped at 1:100,000 scale. The resilience of each stage to flood disturbance was used as our clustering criterion (Table 1 and Appendix S1). We simplified the original dominance-based vegetation distribution from Da Silva *et al.* (2000) into presence/absence information, using a transformation script for ARCVIEW 3.3-ESRI (Redlands, CA, USA). In cases of equal contributions of stages, we set a neighbourhood criterion (based on 'majority rule') so that each planning unit contained just one of the five seral stages at one time, which were used as the starting points for the simulations.

Hydrology and flood dynamics

Wetlands can be classified according to their hydrological, physico-chemical or biological characteristics (Heckman

Table 1 Percentage of the Pantanal covered by different plant communities classified according to their resilience to flooding. Their corresponding spatial distributions are summarized in (Fig. 3).

Classification*	No. planning units	Seral stage	Features clustered†	Resilience	% Area	No. features
Invader	169	Aquatic community	Aquatic habitats	Very high	15	1
Endurer	272	Hydrophytes community	Swampland Floating mats Flooded grasslands <i>Cyperus</i> & <i>Thalia</i> swamps	High	24	4
Resister	93	Wet savanna	<i>Mauritia</i> palm woodland <i>Vochysia</i> forest <i>Copernicia</i> palm woodland Wet Chaco Gallery forest	Medium	8	5
Avoider	360	Dry savanna	Dry grasslands <i>Byrsonima</i> scrublands Savanna scrublands <i>Tabebuia</i> woodlands	Low	32	4
Climax	232	Climax	<i>Orbignya</i> palm woodland Savanna woodland Semideciduous forest	Very low	21	3

*Based on Naiman & Decamps (1997).

†Based on Da Silva *et al.* (2000).

1994a; Lytle and Poff 2004; Robertson and Fitzsimons 2004). Despite several phytosociological studies in the Pantanal which attempt to elucidate some aspects of vegetation and community structure (Prance & Schaller, 1982; Dubs, 1994; Heckman, 1994b, 1998; Pott & Pott, 1994; Pinder & Rosso, 1998; Junk, 1999; Schessl, 1999; Damasceno-Junior *et al.*, 2005), there is scarce information describing the association between vegetation communities and the flood dynamics for this wetland (Heckman, 1994b, 1998; Nunes da Cunha & Junk, 2004). Our succession model based on available floristic information and phytosociological studies attempts to illustrate the relationship between floods and phyto-physiognomies (Adámoli, 1982; Da Silva & Abdon, 1998). The seral stage distribution maps were produced by the aggregation of vegetation maps produced by the Center for Pantanal Research of the Brazilian Agricultural Research Corporation-EMBRAPA (Da Silva *et al.*, 2000), with support from the literature (Pott & Pott, 1994, 2000). Areas converted for pasture within each planning unit were on average smaller than the natural vegetation and therefore were not masked out.

A hundred years of flood data have been recorded for the Pantanal (Hamilton *et al.*, 1996). The pattern found in the Pantanal hydroperiod signature shows fluctuations between short- and long-term flood cycles (Hamilton *et al.*, 2002) that were accredited to stochastic climatic forces (Collischonn *et al.*, 2001; Barros *et al.*, 2004). Based on the correlation found by Hamilton *et al.*, (1996) between river height in Ladário Navy station in Brazil and the flooded area in the floodplain, we spatially interpolated the probabilities of a site being flooded using a geographical information system ARCMAP 9.2 – ESRI (2006). We used the frequency of past flood events, topography and distance to rivers to determine the probability of particular sites being flooded (Fig. 1). We used 394

equidistantly distributed control points in the interpolation and ‘spline with tension’ was the method chosen to generate the flood probabilities for all 1126 sites, because it deals with surfaces, points and topographic features, in a robust manner. We also tested the method for its spatial independency in generating the probability surface used to parameterize our Markovian probabilistic model as prescribed in Drechsler *et al.* (2009).

The biological succession model

We constructed the diagrammatic model of succession for the Pantanal (Fig. 2) considering the relationship between flood regimes, topography (Hamilton *et al.*, 1996), and the probability of vegetation change. The Markovian model of vegetation dynamics underpins the simulations of the probability distribution dynamics through time and its outcome drove the reserve selection process in Marxan (Game *et al.*, 2008). We developed a set of rules used to describe the transitions between the different seral stages. These assumptions based on decades of field observations (Pott & Pott, 1994, 2000) were gathered from a set of sites in the Pantanal floodplain. Those rules describe on average, how many years of disturbance (flood/drought) it would take for a particular seral stage to change to another stage (Fig. 2). The model considers flooding disturbance as an instantaneous event. The maximum level of flooding in a calendar year was used to determine the flood frequency along the time series. For simplification, we overlooked the influence of the duration of flood events on biological succession. However, duration is implicitly considered by the assumption that flood-based biological succession is stochastic rather than deterministic as discussed by the model explanation in Drechsler *et al.* (2009).

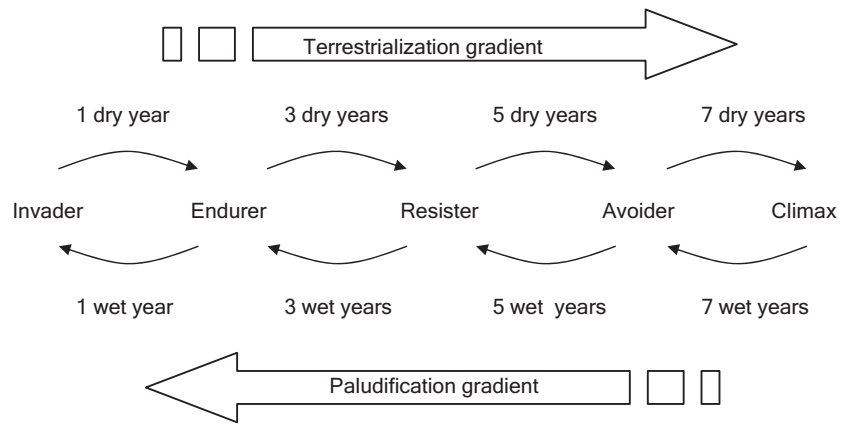


Figure 2 Logical model for the transition rules between the different succession stages and the transition time necessary for a community to change between stages measured in years (Drechsler *et al.*, 2009).

Predictions were based on the flood probability of individual planning units. To implement the model, we assumed a ‘flooding as usual scenario’ whereby flood events will be stochastic but flood frequencies will remain relatively unaltered. This approach assumes that a climate similar to that of the last century will be influencing the Pantanal over the coming 50 years. Therefore, each site has a certain probability of being flooded (q) in a particular year. Estimates of these probabilities were based on 100 years of records of past floods (Hamilton *et al.*, 1996). We constrained the problem by assuming that each site may be occupied by just a single community at the beginning of the simulation (Drechsler *et al.*, 2009). Then we constructed a Markov chain model of

vegetation succession to determine the probability p_{ij} of observing a particular state j at a given site i in the future, under the assumption that flood frequencies in the future would remain the same as they have been between 1900 and the present.

We used distribution maps of the presence or absence of our five seral stages (Fig. 3) as seeds for the Markov chain simulation routine in MATLAB (MathWorks, Natick, MA, USA), with the purpose of predicting the future state of the system (i.e. spatial distribution of our successional stages) (Balzter, 2000). Our objective for the Pantanal reserve system was to spatially capture a fixed fraction of each existing seral stage with maximum reliability (i.e. minimum uncertainty) of

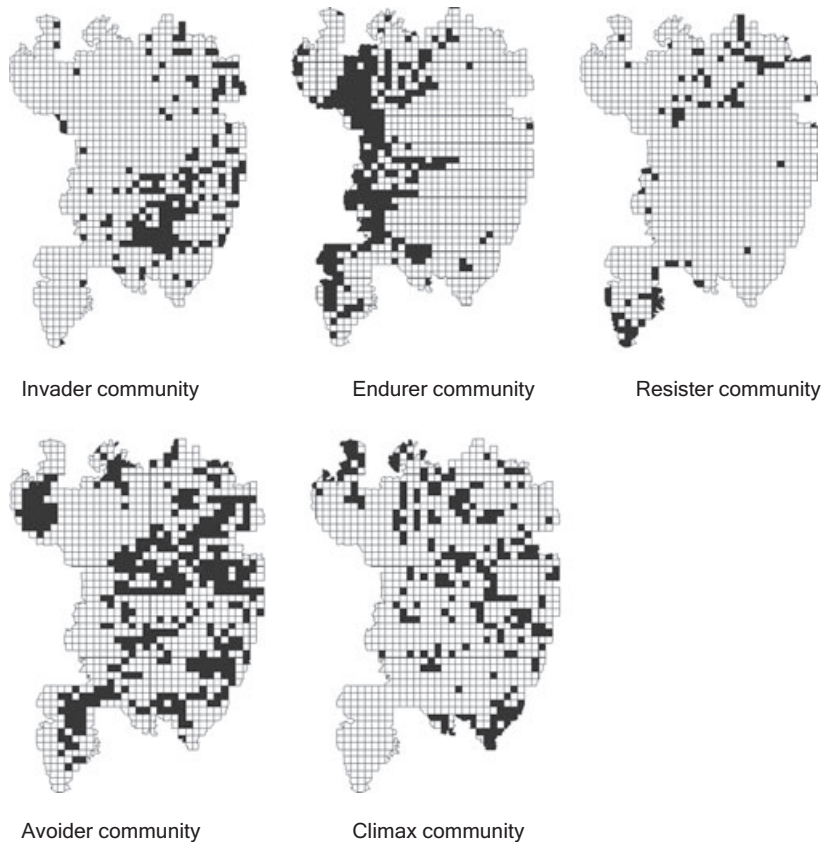


Figure 3 Maps of the distribution of the five succession stages in the Pantanal floodplain, re-sampled from Da Silva *et al.* (2000) as described in Table 1.

retaining representation in the future. We assume that our Markovian probabilistic model adequately describes (Drechsler *et al.*, 2009), and is able to simulate, the successional processes that will occur in planning units spread across the floodplain (Appendix S2). After the data pre-processing, the outcomes of simulations consisted of a probability matrix where each planning unit has a certain likelihood of being at each seral stage 50 years later, based on flood history.

Simulated time to reach stationary distribution of seral stages in the Pantanal

To understand the applicability of the Markovian simulations to conservation planning, it is necessary to understand the behaviour of the model through time. Markov chains are known to reach a stationary distribution, which is an essential assumption and could limit the viability of the model predictions for conservation purposes (Facelli & Pickett, 1990; Junk *et al.*, 2006). We used sensitivity analysis to elucidate the effect of time on the hydrosere model. We simulated the succession behaviour 200 years into the future to evaluate the stabilization point and its appropriateness for conservation planning. Running simulations, we found that each seral stage stabilized at slightly different timeframes; however, results indicated that the 50-year stabilization point is appropriate and realistic for long-term conservation planning (Fig. 4). This supports the use of the model (Drechsler *et al.*, 2009) in real-world planning, while still consistent with assumptions of spatial independency for the hydrosere model (Burgman, 2005).

The problem of site selection in dynamic systems

We investigated the capacity of our disturbance model to predict the future distribution of seral stages, evaluating the effects of succession dynamics on the selection frequency of planning units across a series of planning horizons, from now to 50 years. We set targets for each of the five seral stages under the minimum set coverage problem (Possingham *et al.*, 2000; Moore *et al.*, 2003). Solutions are expected to maximize the likelihood of target representation at a minimum cost.

Flood probabilities for each planning unit were derived from topographic maps and the major hydrological network and divided into 10 intervals, according to the flood frequency chart thresholds for community change (Fig. 2). This decision limited the scale of analysis to planning units of 10,000 ha, what can be considered a coarse scale for habitat mapping but enough to represent average property size, and therefore a management unit.

We evaluated these matrices over four simulated timeframes: 5, 17, 25 and 50 years. Nevertheless, to conform to the assumption of spatial independence, just two scenarios were used to evaluate adequacy: the present conditions (5 years) and the end of our planning horizon (50 years). Marxan software was used to select planning units that maximized the probability of representing 20% of the extent of each of the five seral stages over the entire planning timeframe, based on current and projected distributions. The cost considered was described in Drechsler *et al.* (2009), a programming method that provided an exact solution to the problem of selecting sites under stochastic disturbance. Despite being initially complex and computationally demanding the parameterization and implementation of the method, a probabilistic approximation proposed by the same authors, based on spatial independence between sites (Appendix S3), allowed the efficient exploration of solutions using the existing Marxan software represented by the number of planning units recruited in each solution (<http://www.uq.edu.au/marxan/>) (Game *et al.*, 2008).

Sensitivity analysis

As our aim was to verify the effect of spatiotemporal heterogeneity on planning unit selection, we used a modified version of the Marxan decision support system (Ball & Possingham, 2000; Drechsler *et al.*, 2009) to incorporate disturbance risk into the site selection problem using the Pantanal wetland flood probability surface. The sensitivity of site selection to simulated changes in community dynamics was tested over four planning timeframes with the aim of adequately meeting our targets for representation, both in the present and at the end of a 50-year planning horizon. We use the term 'reliability' to refer to the probability of achieving our targets.

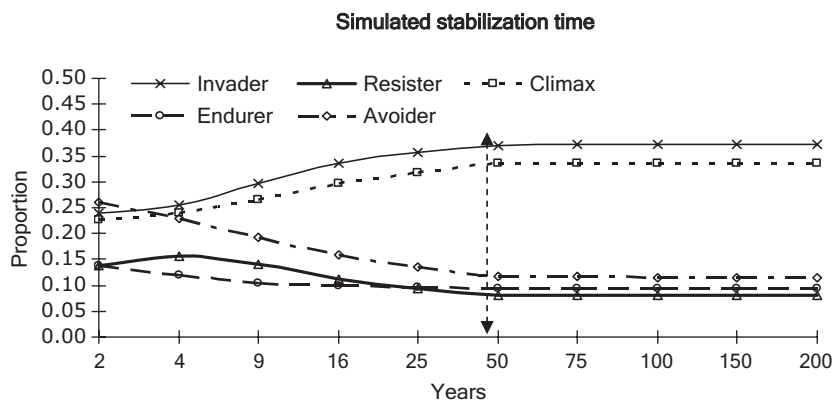


Figure 4 Sensitivity analysis of Pantanal hydrosere simulated through time using the proposed Markovian model of transition probabilities. The arrow marks the point in time where the probability distribution of each seral stage reaches its stationary distribution.

To investigate the effect of reliability requirements on the efficiency of solutions, we tested interval between 50% and 100% reliability, here the least number of planning units in a solution the more efficient the solution was (Pressey & Nicholls, 1989). Each Marxan solution was the average of 100 runs of 1,000,000 iterations each. The ‘summed solution’ output was assumed to be a measure of the irreplaceability of each planning unit (Carwardine *et al.*, 2007). We then verified the reliability level of such solutions for each planning timeframe (Fig. 5). We used the Kappa statistic to conduct pairwise comparisons between solutions to evaluate how dissimilar solutions were after the removal of overlaps because of chance, between different planning timeframes (Monserud & Leemans, 1992; Richardson *et al.*, 2006).

RESULTS

Hydroperiod and flood dynamics in the Pantanal

Considering the extent of the Pantanal wetland (140,000 km²), the annual probability of a flood larger than 100,000 km² (80% of the floodplain size) is 7% over the last century (Fig. 1). Flood events, spanning more than 80,000 km² (i.e. 60% of the total floodplain area), were the most frequent, occurring 26% of the time, while the average flood size, covering 53,000 km² occurred only 5% of the time (Hamilton *et al.*, 1996). These results point to a frequently disturbed ecosystem, where

processes and functions are often determined by climatic stochasticity as described in the literature (Assine & Soares, 2004; Junk *et al.*, 2006).

Trade-offs between reliability of predictions and the efficiency of reserve systems

Considering that we were not interested in solutions that have low probability of securing future representation, we constrained our search to the 50% and 100% reliability intervals and over the 50 years planning horizon. We explored this interval to achieve target representation in the most efficient/reliable way possible using Marxan’s annealing algorithm.

The behaviour of selection frequency (i.e. irreplaceability score) for individual planning units was quite intriguing (see Fig. 5a–g). At a lower reliability requirement, the irreplaceability of each site is ambiguous with the majority of planning units selected with almost equal (low) frequency. As the penalty for missing targets in the future was increased, the solutions become more focused, with some planning units showing a markedly higher irreplaceability score (Fig. 5f).

However, if we wish to achieve conservation goals with very high reliability (i.e. > 90%), most planning units became highly irreplaceable, and solutions became costly and inefficient. In summary, as reliability requirements increase, the number of planning units necessary to meet targets in the

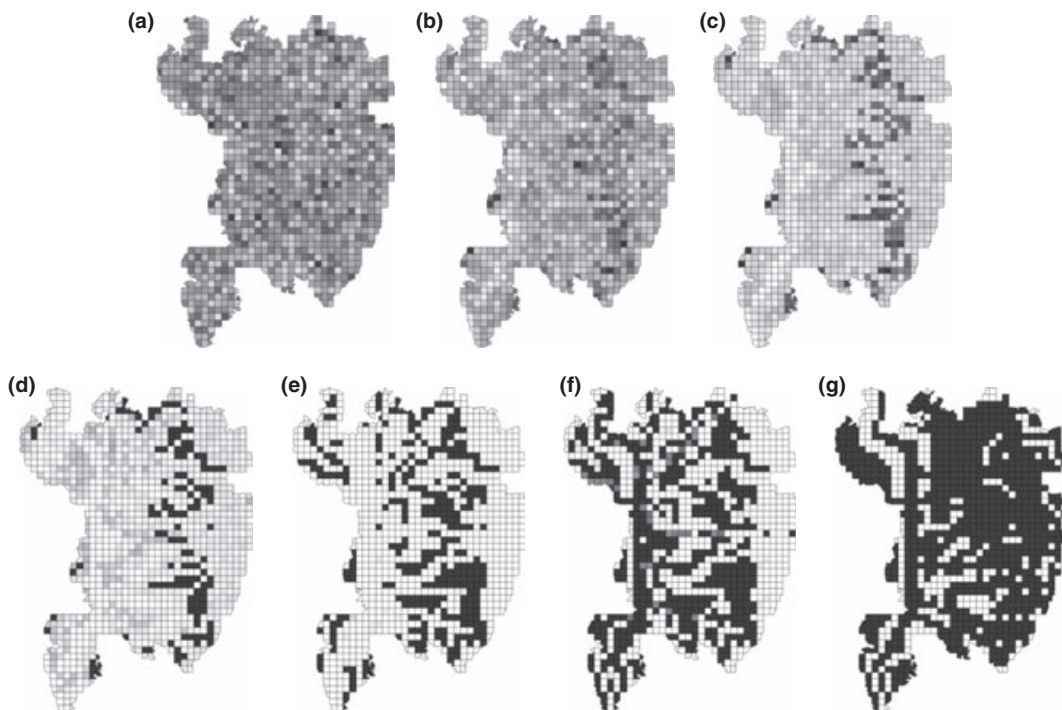


Figure 5 Sensitivity analysis of planning unit selection frequency (irreplaceability) according to demand for reliability for the 50-year planning timeframe. Here, figures (a–g) represent an automatic calibration of exponential increases in weights, to explore the solution space between 50% and 100% of expected reliability of achieving the 20% target for all successional stages in a 50-year timeframe.



Figure 6 Changes in the spatial distribution of selection frequencies of planning units (darker grey represents higher irreplaceability) to represent the 20% of all five seral stages in the Pantanal. For (a–c) achieved 95% reliability, respectively, for 5, 17, 25 years, whereas 50 years into the future, a very efficient solution (d) has a reliability of 88%.

future (i.e. cost) grew exponentially (Fig. 7). In our case study, a solution with 90% reliability required 850 planning units, however, we still found at 88% reliability highly efficient solutions (225 planning units).

Analysis of selection frequency through time

The Kappa statistic indicated that there was little spatial similarity between solutions for any of the four time steps considered so planning for different times in the future requires quite different plans. Spatial similarity is a metric that ranges from 1 to -1 (Table 2), where one equals a 100% similarity between solutions while a value of 0 means that similarities were no bigger than what would be expected by chance alone. If the value approaches -1 , the results are considered highly dissimilar (Fielding & Bell, 1997). All values were very close to 0 (i.e. from -0.0675 to 0.253) indicating

that similarities between solutions are not statistically different than those because of chance (Table 2). The results strongly suggest that the dissimilarity between selection frequency maps was driven by two factors. For short-term plans of < 5 years (Fig. 6a), selection frequency scores respond to the spatial distribution of features alone, because the state of the vegetation in each planning unit does not change significantly in such a short time period. Beyond 5 years, the effect of simulated transitions starts to operate (Fig. 6b,c). However, at 50 years when the stationary distribution is reached, the effects of spatial autocorrelation become negligible, as predicted by the model. Site selection then becomes driven by the biological succession dynamics, which is heavily influenced by the flood history of the site (Fig. 6d), and the majority of highly irreplaceable planning units are found in regions where the highest frequency of historical disturbance occur.

Figure 7 Trade-off curve for the 50-year planning horizon. The plot shows the reliability of each solution on (*x*) axis and cost (measured in number of planning units taken by each solution) on the (*y*) axis. The arrow shows the solution with the best trade-off between reliability and efficiency.

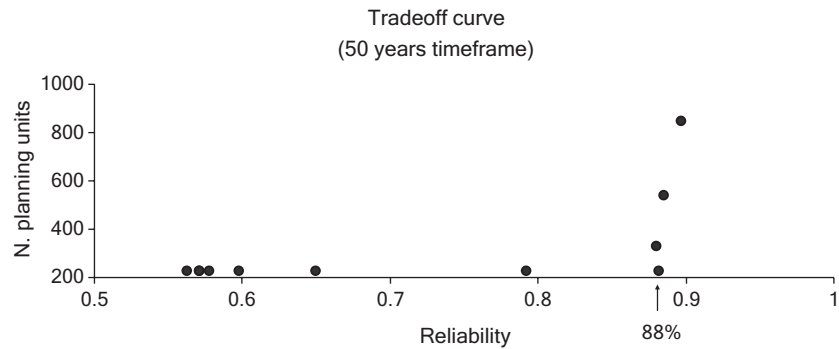


Table 2 Pairwise comparison of planning timeframes, using the Kappa statistics values for Marxan's summed solution outcomes (Monserud & Leemans, 1992).

Timeframe (in years)	5	17	25	50
5	1	0.0695	-0.0675	0.0121
17		1	0.208	0.0897
25			1	0.253
50				1

DISCUSSION

Systematic conservation planning aims for comprehensive, adequate, representative and efficient protection of the Earth's biodiversity (Possingham *et al.*, 2006). Very few conservation plans, however, explicitly consider the natural temporal dynamics that most ecological communities experience. This is despite an extensive and well-documented knowledge about the importance of temporal heterogeneity in shaping biotic communities (Clements, 1936; Odum, 1983). Designing reserve systems that adequately represent biodiversity now and in the future under such dynamic conditions is a challenge for three reasons: the unpredictability of climate into the future; the lack of understanding of succession pathways; and the uncertainty around the ability of models to predict changes (Leroux *et al.*, 2007a).

Here, we addressed the problem of incorporating disturbance dynamics in conservation planning to better enable reserves to meet both current and future conservation goals. This was achieved by allowing the treatment of disturbance dynamics, based on Markov probability chains, to be used in a spatial optimization method. This treatment enabled us to deal with the uncertainties associated with predictive modelling, while also providing statistical robustness and flexibility for the decision-making process.

The results presented here demonstrate that the spatial distributions of conservation priority can be markedly different when different planning timeframes are considered (Fig. 6). Our results suggest that short-term plans based entirely on current distribution of features can lead to inadequate conservation outcomes. Given this is true for a simple 'flooding as usual' scenario, the adequacy of existing reserves

under the potential effects of climate change and water diversion may be even further compromised.

The design of reserve networks that consider temporal dynamics depends not only on our ability to predict future changes, but perhaps more importantly, on the level of reliability demanded of these predictions and our subsequent decisions. The easiest way to achieve greater reliability is through the acquisition of more planning units (see Fig. 7) such that demanding more reliable outcomes is likely to result in more expensive reserve systems. In the Pantanal case, where plans that are based on stewardship mechanisms (i.e. little budget restrictions) and concerned with the future adequacy, we might choose highly reliable but spatially inefficient solutions. If however, there are limited resources (e.g. when there are true acquisition costs involved), planners might choose the least expensive systems, compromising somewhat on the reliability with which they meet conservation targets.

Considering temporal dynamics in conservation planning requires appropriate planning horizons, this will require finding the balance between practicality and predictive reliability. We can predict with a good degree of reliability what the distribution of the vegetation types will be in 1 year's time. However, no one would suggest that it is practical or desirable to re-design a reserve network every year as successional changes occur. On the other hand, a 100-year plan may be politically appealing; most scientists will feel uncomfortable making environmental predictions over that timeframe.

Our ability to reasonably predict the future in dynamic systems and thus find good indicators of an appropriate planning horizon will depend on the type and speed of expected ecosystem changes and the amount of information available on such dynamics. The corollary of accepting the outcomes of such predictive exercises is that the best solutions are reliant on the resources needed to implement them and how confident stakeholders need to be.

Implications for conservation planning

To date, the literature has not offered a convincing solution to the problem of incorporating freshwater dynamics as part of the reserve selection process, and how it affects the principle of Adequacy. Post hoc approaches such as the one suggested by Leroux *et al.* (2007a) definitely help to design adequate reserve

systems and to adjust them to cope with an ever changing environment. However, using a new problem formulation coupled with a stochastic vegetation succession models enabled us to find reserve systems that meet both current and future conservation objectives in an optimal, defensible and transparent way. This is one of our method's advantages when compared to niche-based modelling and scenario building (Carroll *et al.*, 2010). The adaptations introduced in the reserve selection software Marxan enabled it to deal with probabilistic datasets in a robust manner, therefore, generating solutions that are reliable and realistic. However, the greatest advantage of our method is that it offers the opportunity to make decisions today that will, under acceptable levels of uncertainty, give a high probability of achieving targets into the future.

Model limitations

The results presented here are based on a highly simplified view of the Pantanal succession dynamics, including the use of discrete time, which forces the model to behave in a stepwise fashion rather than a continuous process. Nevertheless, animal and plant communities often respond to seasonality in a stepwise fashion, buffering effects caused by the hydroperiod dynamics (Clarke, 2005). Transitions between seral stages are then determined by the cumulative effect of subsequent years of floods or droughts and can occur for early stages of succession based on one seasonal cycle, or several years for the later stages. As a consequence, flood history has good explanatory and predictive power on how succession is pushed through these transition thresholds. More complex succession trajectories are not uncommon (Van Hulst, 1979) and the model could be adapted to simulate such trajectories.

For simplicity, we also ignored the influence of other factors that may affect succession such as soil composition, biogeography, damming, intensive grazing and fire. Some of these factors can be simultaneously approached in Markovian submodels. Nevertheless, the advantages of using Markovian approaches to handle temporal stochasticity in reserve design applications greatly surpass their limitations. First of all, Markovian models use probability as their currency, allowing uncertainty to be explicitly considered. Also because of their computational simplicity, they allow direct tests of the length of a system's memory and determination of the stationary distribution. Finally, they can handle a large number of variables and have a diverse apparatus for robust statistical inferences (Horn, 1975). In combination, these features allow straightforward integration of both spatial and temporal heterogeneity into systematic conservation planning.

Implications for conservation in the Pantanal wetland

The existence of carryover effects from subsequent floods has clear effects on species diversity and abundance (Clarke, 2005). Empirical data suggest that these effects are particularly important for recruitment and survival in fishes and reptiles

in the Pantanal (Coutinho & Campos, 1996; Catella *et al.*, 1999). Our simulations indicate they are also essential for plant communities and should be considered in any effort to protect biodiversity in the Pantanal.

The results of this study indicate that designing reserve systems to simply represent present-day vegetation classes in wetlands such as the Pantanal without incorporating the likelihood of change because of flooding and succession is inadequate. Conservation priority maps that do incorporate successional dynamics differ dramatically from those based only on the current distribution or their likely succession of vegetation through time. Some emergent rules-of-thumb are as follows: (1) planning timeframes should reflect the timeframe of ecosystem process under study; (2) if the system is subject to disturbances, understanding its frequency improves the adequacy of conservation plans; and (3) when spatial autocorrelation is not present, protecting the areas frequently disturbed apparently increases the likelihood of reserve system adequacy in the Pantanal.

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SUPPORTING INFORMATION

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

Appendix S1 The characteristics of the five seral stages which described the starting points of simulation as shown in Fig. 3.

Appendix S2 Mathematical formulation and the description of the model properties.

Appendix S3 Statistical formulation and model properties behind the adaptations of the Decision support software Marxan.

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BIOSKETCH

Reinaldo Lourival has a background in ecology and wildlife management, more recently focused his research into systematic conservation planning, with interest in the dynamics of habitats and tropical wetland ecology. His aim is to expand the capabilities of decision support software as a tool to investigate how conservation decisions can be improved in the Tropics. Reinaldo is currently working in the identification of partial contribution of biodiversity in different land use types into systematic zoning, aiming to improve the UNESCO's Biosphere reserve concept and accountability, through further developments of Marxan decision support software.

Author contributions: R.L. conceived the idea for the paper, gathered and analysed the data, and led the writing; M.D. formulated the mathematical problem and tested a simplification method to handle the issues of spatial autocorrelation. M.W. and E.G. developed the Marxan algorithm to manage probabilistic dataset. H.P. in the capacity of supervisor guided the collaboration process and provided insights and with E.G. reviewed the manuscript helping increase the paper focus.

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