Modelling Effects Of Secondary Salinisation On Wetland Biodiversity

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Keywords: *Ecosystem modelling; adaptive management; salinity; wetland; biodiversity.*

EXTENDED ABSTRACT

The clearing of natural vegetation and irrigation for farming have resulted in rises in the level of groundwater. The rising water table brings salt previously stored deep in the soil profile to the surface, leading to secondary salinisation. Whilst many ecosystems are affected by secondary salinisation, wetlands are considered to be particularly vulnerable because of their low-lying position in the landscape where they are likely to be quickly affected by the rising saline water table as well as catchment runoff. Secondary salinisation may induce the regime shift in wetland ecosystems and is one of the greatest threats to our wetlands.

We have developed a mathematical model to explore possible effects of secondary salinisation on wetland biodiversity. The model provides a conceptual framework for the characterisation and classification of wetlands under the impact of secondary salinisation. The model predicts two possibilities of stability in wetland biodiversity: monostability and bistability. Bistability can give rise to a discontinuous abrupt response of a system to a continuous small change of a driving factor. Factors that influence changes in biodiversity include salinity, other wetland conditions, and the initial biodiversity state. All of the driving factors exhibit threshold effects. The response of the equilibrium biodiversity to changes in one driving factor will vary depending on other driving factors as well as the history of the system. The model suggests that wetlands can be classified into two types on the basis of their dynamics. The two types of wetlands are fundamentally different systems. They exhibit different ecological responses to changing salinity: The response of wetlands of type 1 occurs in a graded fashion, whereas wetlands of type 2 produce a hysteretic response. For a range of intermediate levels of salinity, two stable states of biodiversity coexist in the wetland of type 2 under identical physical, chemical and biological conditions (including salinity).

This simple model provides meaningful insights into the salinity issues and predicts how the system can and cannot behave, given the assumptions that wetland biodiversity will stabilise and secondary salinisation acts as a disturbance and reduces biodiversity. The model guides the selection of biodiversity measures as these have to show clear responses to salinisation. The model is empirically falsifiable and thus allows progress in scientific study. The adequacy and accuracy of the model as an approximation to the real, complex world can be tested by testing the model's assumptions and confronting the predictions with natural observations and experimentation. Eventually, both qualitative and quantitative understanding of how biological, physical and chemical processes interact to shape the wetland's biodiversity, gained from combining modelling with empirical data collection, will substantially enhance the predictive capacity regarding the management of wetlands threatened by secondary salinisation.

The management of wetlands threatened by secondary salinisation has two distinct focuses: (1) the preservation and protection of pristine wetlands and (2) the restoration of degraded wetlands. The effectiveness of management for biodiversity depends on where the system is in the biodiversity landscape. The key for the preservation and protection of the wetland with high biodiversity is resilience of the system—the maintenance of biodiversity despite fluctuations in the behaviour of its component parts or its environment. In reality, the system and its environment inevitably contain many sources of noise. To be safe, any pristine wetland must have its stable state at a prudent distance from the thresholds. Resilience gives the wetland the flexibility to respond to different kinds of uncertainties and extreme events and ensures that the wetland can withstand them. On the other hand, the key for the restoration of a wetland with low biodiversity is sensitivity of the system—the possibility of a large response to small perturbation—so that the degraded system is easy

to restore by management actions. Our model suggests that the two types of wetlands demand different management strategies.

1. INTRODUCTION

Despite repeated observations over more than 50 years that increasing salinities are having devastating effects on natural ecosystems (Briggs and Taws 2003), environmental management is still hampered by a lack of knowledge of how such systems respond to salinisation (Blacklow 2003). Wetlands, in particular temporary and permanent bodies of still waters, are particularly neglected in terms of assessing the ecological effects of changes in salinity levels associated with human activities, and it has been suggested that secondary salinisation poses a serious threat to Australian wetland biodiversity (Davis et al. 2003; James et al. 2003; Cale et al. 2004; Pinder et al. 2004).

Secondary salinisation is a problem created by people, and now has become an urgent management target (Council of Australian Governments 2000). However, given the limited amount of knowledge about the effects of secondary salinisation in wetlands and the effectiveness of associated management, a structured modelling approach is likely to provide a way forward in suggesting possible management approaches. Here we have adopted a rigorous modelling approach to represent existing ecological knowledge and explore management options for wetlands that may be deleteriously affected by secondary salinisation. The approach we have adopted is based on a rigorous adaptive management framework and can result in targeted management to fill further knowledge gaps (Schreiber et al. 2004). The basic assumptions behind this exploratory modelling approach are that the biodiversity of a wetland will reach stability and secondary salinisation represents a perturbation that results in a disturbance to wetland ecosystems and lowers wetland biodiversity. The last assumption forms the basis for a current initiative by the Australian Government to combat the effects of secondary salinisation on Australian ecosystems and production systems (Council of Australian Governments 2000).

We adopt a holistic approach to construct a mathematical model to capture dynamic features of wetland ecosystems under the impact of secondary salinisation. We assume that wetland biodiversity will stabilise and secondary salinisation acts as a disturbance and results in a decline of system-level properties, specifically biodiversity. We use the model to develop an understanding of these system-level properties and emergent behaviour. The model quantifies the state and dynamics of wetland biodiversity by taking into account the interaction of biodiversity with secondary salinisation. In order to explore what might happen under different circumstances, we systematically analyse the dynamic behaviour of wetland ecosystems by considering a space of possible systems in the complete range of parameters and, in particular, the system's response to various salinity levels. We aim to identify what factors influence the biodiversity of wetlands and to predict the change of the biodiversity state as these factors are changed by either natural events or human intervention. Our goal is to use the insights and conceptual development gained from this research to provide new ideas and innovative methods for empirical tests that are likely to improve the management of wetlands and minimise the potential loss of biodiversity.

2. MODEL

In general, we assume in the model that the biodiversity of a wetland evolves according to the equation

$$\frac{d\psi}{dt} = D(\psi) - S(\psi), \qquad (1)$$

where the variable $\psi(t)$ measures the biodiversity state of the ecosystem at time *t*, which may represent species richness or some other index of biodiversity. Both time and the state space are continuous. $D(\psi)$ represents the contribution to the rate of biodiversity change in the absence of disturbance. Several interacting ecological processes, which include survival, reproduction, migration, competition, facilitation, and predation, are described by $D(\psi)$. Given that salinity is thought to interfere with basic ecological functions and affect food supply, available habitat, or breeding grounds in wetlands (Williams 1999), secondary salinisation is likely to have an advert effect on wetland ecosystems, causing biodiversity loss. $S(\psi)$ denotes the term incorporating the interaction between wetland biodiversity and secondary salinisation. The complexity of wetland ecosystems is hidden in part in $D(\psi)$ and $S(\psi)$. The functional forms of $D(\psi)$ and $S(\psi)$ regulate the biodiversity dynamics.

A range of ecological theories and concepts suggest a variety of biological, physical and chemical conditions and processes that may determine wetland community structure (Zedler 2000). It has been suggested that physical and chemical factors often operate at large scales (e.g., climate or nutrients), whereas many biological factors, such as competition and predation, act at local, individual organism scales (Menge and Olson 1990). The niche concept, re-defined by Hutchinson (1958), differentiates between a fundamental niche, describing a set of environmental resources that a species can survive in and a smaller, realised niche that includes the resources a species uses in the absence of competition and other biotic interactions (Krebs 2001). For the purpose of modelling wetland dynamics we assume that the biodiversity of a wetland would, in the absence of disturbance, have a stable state determined by its physical, chemical and biological conditions. Furthermore, the natural, undisturbed rate of biodiversity change is assumed to be zero at $\psi = 0$, increase for small ψ, reach a positive maximum at some value of ψ, and decline thereafter. A specific form of $D(\psi)$ that incorporates these assumptions is

$$D(\psi) = r\psi^m \left(1 - \frac{\psi}{K}\right), \qquad (2)$$

where *r, m* and *K* are positive parameters. As a result, $\psi = K$ is the stable state of biodiversity in the absence of disturbance. The parameter *r* determines how fast the system approaches the stable state. The parameter *m* specifies the location where the rate of biodiversity change in the absence of disturbance reaches its maximum.

No interaction between wetland biodiversity and secondary salinisation can happen when there is no biodiversity at all. The strength of the interaction is assumed to increase as the biodiversity increases and saturate for sufficiently high biodiversity. Thus, we assume that $S(\psi)$ takes the form

$$S(\psi) = \alpha \frac{\psi^n}{\psi^n + h^n}, \qquad (3)$$

where α, *n* and *h* are positive parameters. The parameter α designates the strength of the interaction between wetland biodiversity and secondary salinisation. $S(\psi)$ reaches half saturation when $\psi = h$; that is, $S(\psi) = \alpha / 2$ at $\psi = h$, while $S(\psi) = \alpha$ as $\psi \to \infty$. The parameter *n* regulates how fast the interaction between wetland biodiversity and secondary salinisation saturates with biodiversity.

Substituting (2) and (3) in (1) and introducing the rescaled quantities $X = \psi / h$, $\tau = h^{m-1}rt$, $k = K / h$ and $s = \alpha / (rh^m)$, we obtain the governing equation for the wetland biodiversity in dimensionless form

$$\frac{dX}{d\tau} = X^m \left(1 - \frac{X}{k}\right) - s\frac{X^n}{X^n + 1}, \qquad (4)$$

which is dynamically equivalent to (1)-(3). The rescaled biodiversity measure *X* is expressed as a function of the four dimensionless parameters *k, s, m, n*.

The parameters *k* and *s* capture the essence of the system dynamics. The parameter *k* is effectively a measure of "wetland quality", which we have defined here as characterising its physical, chemical and biological conditions in the absence of disturbance. It might typically be a function of underlying measurable quantities such as water depth, area, temperature, nutrients, alkalinity, pH, turbidity, etc., and thus might vary widely. Provided that no disturbances occur, the larger the value of *k*, the higher is the biodiversity at the stable state. The coupling parameter *s* gauges the strength of the interaction between wetland biodiversity and secondary salinisation. It is generally a function of the total ionic concentration and we assume that it is proportional to total ionic concentration. The remaining two parameters *m* and *n* characterise more detailed dynamics of the system. In the present work we focus on the exploration into the general characteristics of wetland biodiversity dynamics under the impact of secondary salinisation where secondary salinisation acts as a disturbance. We will not discuss more detailed dynamics and set the two parameters to be $m = 1$ and $n = 4$ in our analysis. In the end, comparison with real empirical data is the only test of a theory or model. The model parameters can be extracted by fitting the model to measured biodiversity values at different levels of salinity and wetland conditions.

3. RESULTS

The long-term dynamic behaviour of wetland biodiversity under the impact of secondary salinisation can be inferred from stability analysis by using (4) and setting $dX/d\tau = 0$. After some transient state, a wetland ecosystem will for a long time be found resting at a stable steady state. The model predicts that stability in wetland biodiversity has two possibilities—monostability and bistability—depending on wetland conditions. For certain values of the parameters, wetland biodiversity exhibits monostability, whereby all initial states (except the unstable steady state, which remains constant) exponentially approach a unique, globally stable steady state. For other values of the parameters, wetland biodiversity exhibits bistability—two locally stable steady states coexist under identical physical, chemical and biological conditions, and the state on which the system settles will depend on its initial state or history.

The parameter space is shown in Fig. 1, where the monostable and the bistable region of parameters are indicated. The system described by the values of the parameters lying in the bistable region is bistable; otherwise, the system is monostable. The boundaries between the monostable and the bistable region correspond to specific combinations of salinity and other wetland conditions. They define the threshold set of parameters for the transition between monostability and bistability.

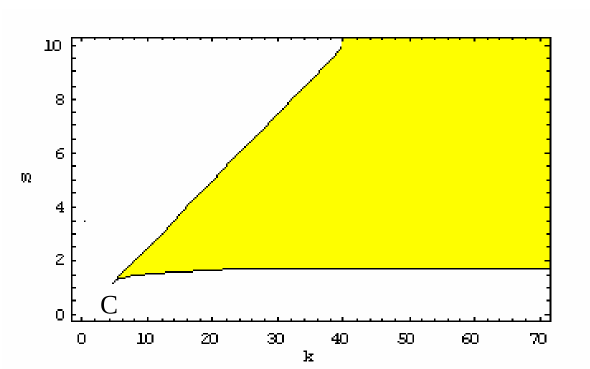

Figure 1. Theoretical parameter space of wetland ecosystems. The shaded region is the bistable region. The other region is the monostable region. The region of bistability becomes smaller as the parameter *k* decreases, eventually reaching the cusp point (C) with the critical values (k_c, s_c). The critical values of *k* and *s* are $k_c = 4.55$ and $s_c = 1.19$ for the default values of the parameters $m = 1$ and $n = 4$.

The relationship between the equilibrium biodiversity and salinity and other conditions of wetlands can be derived from the model. By examining the dynamics for the complete range of parameters we obtain an overview of how the system behaves. Figure 2 shows the equilibrium biodiversity as a function of the parameters *k* and *s*. The horizontal plane is the parameter space as in Fig. 1. The third dimension corresponds to the equilibrium biodiversity. In the three-dimensional picture the equilibrium biodiversity lies on a surface—a landscape across which the equilibrium biodiversity is forced to move.

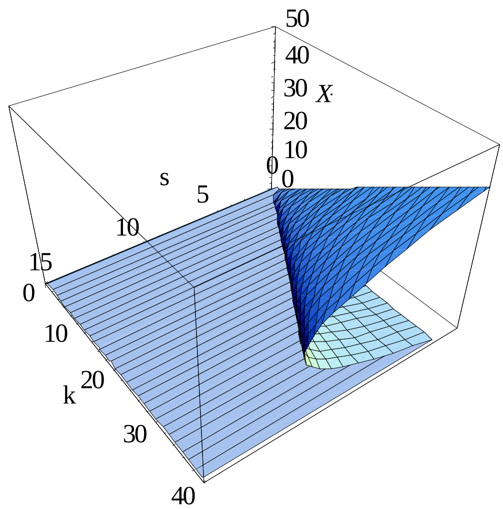

Figure 2. Equilibrium biodiversity as a function of the model parameters *k* and *s*.

We can see explicitly from Fig. 2 that in our model wetland biodiversity has a single stable state in the monostable region (the unfolded surface), and the equilibrium value of biodiversity is uniquely determined by the parameters *k* and *s* regardless of initial states. In the bistable region (the folded surface), wetland biodiversity has two possible stable states—one in the upper sheet and the other in the lower sheet, and the selected stable state is determined not only by the parameters *k* and *s*, but also by the initial state. The unstable steady state lies on the middle sheet of the folded surface. Any initial state that starts exactly on it will stay fixed forever, but the slightest disturbance will cause it to repel out and away. The unstable middle sheet acts like a biodiversity threshold and partitions the state space into regions of different long-term behaviour. All the initial states above it move to the stable upper sheet, while all the initial states below it move to the stable lower sheet.

With gradual changes in the parameters, the equilibrium wetland biodiversity may move smoothly along the surface. However, at certain thresholds for *k* and *s*, an abrupt, discontinuous change in biodiversity may occur between the upper and lower sheet. The threshold set shown in Fig. 1 is where this discontinuity takes place in the parameter space. Note that if the parameters *k* and *s* vary along a path avoiding the threshold set altogether the transition between the bistable states will be perfectly smooth as the upper and the lower sheet merge gently beyond the equilibrium biodiversity corresponding to the cusp point $\left(k_c, s_c\right)$. Thus, bistable states can sometimes blend continuously into each other. In the bistable region, a change in the initial state of biodiversity crossing the unstable middle sheet may also result in the system evolving from one stable state to another.

We identify the factors that drive the biodiversity change to be salinity, other wetland conditions, and the initial biodiversity state. Salinity and other wetland conditions will always affect the stable state. However, only in the bistable region can the initial biodiversity state have a role to play. Our model shows generally how biodiversity behaves as these factors change individually or simultaneously (Fig. 2). We now investigate specifically how changes in wetland biodiversity take place in the special case that only salinity varies and all other conditions remain unchanged. This special case is just one part of the overall picture (Fig. 2), obtained by projecting the biodiversity landscape onto a plane with constant *k*.

We can see from Fig. 1 that bistability is possible to appear only for $k > k_c$. It follows that we can classify wetlands into two types according to their physical, chemical and biological conditions in the absence of disturbance. The critical value k_c separates two types of wetlands. Type 1 wetlands are those with low values of *k* ($k < k_c$), while type 2 wetlands are those with high values of *k* ($k > k_c$). In our model these two types of wetlands exhibit qualitatively different responses to changes in salinity (Fig. 3).

Type 1 wetlands have low biodiversity even in the absence of disturbance. Because of low values of *k*, which represents low wetland quality (likely to be associated with low levels of resources and poor biological conditions), the change of the biodiversity state of type 1 wetlands is smooth with a gradual change of salinity (Fig. 3a). This type of model wetlands undergoes a successional process as salinity changes. As salinity increases, biodiversity of type 1 wetlands decreases monotonically. There is a single stable state of wetland biodiversity for a fixed value of salinity, to which all states of wetland biodiversity eventually converge. Thus, changes in the initial state have a temporal effect and cannot affect the long-term biodiversity state of the type 1 wetland. Physical, chemical and biological conditions are the only factors that influence the biodiversity state of the type 1 wetland.

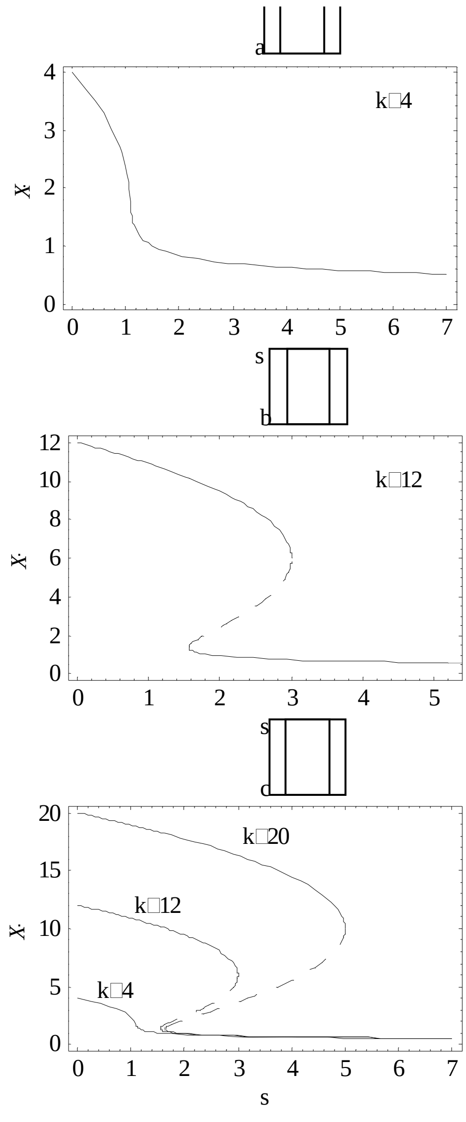

Figure 3. Response of the equilibrium biodiversity to changing salinity for (a) the wetland of type 1 with constant *k*, (b) the wetland of type 2 with constant *k*, and (c) both types of wetlands with various values of *k*. The dashed lines represent the unstable steady states, marking the biodiversity thresholds.

By contrast, type 2 wetlands are rich and complex. They have high biodiversity in the absence of disturbance. High values of *k*, which represents high wetland quality (likely to be associated with high levels of resources and good biological conditions), promote biological complexity, response diversity, and functional redundancy of the ecosystem, making it resilient to perturbation. The model dynamics of type 2 wetlands under the impact of secondary salinisation is more complex than type 1 wetlands. Our modelling suggests that wetlands of type 2 possess the following properties (Fig. 3b):

- Bistability. At low salinity levels the wetland will have a single stable steady state with relatively high biodiversity, while at high salinity levels the wetland will have a single stable steady state with relatively low biodiversity. However, at intermediate salinity levels the wetland has two stable states of biodiversity, one with a high and one with a low biodiversity. That is, there are two discrete stable steady states for a single value of salinity.
- Threshold salinity. There are two thresholds for salinity. Stable states split up or disappear as salinity moves across a threshold. As long as they are not reached, changing salinity has small effect on biodiversity. However, if thresholds are crossed in a certain direction, a substantial, discontinuous change in biodiversity can take place, following a minute, continuous change in salinity. The biodiversity will suddenly collapse from a high value to a low value at the collapse threshold, while the biodiversity will suddenly shift from a low value to a high value at the recovery threshold. The range of salinity between the collapse and the recovery threshold is the bistable region where two stable states coexist in the system. At a single value of salinity within the bistable region, the system can be either in a low-biodiversity equilibrium or in a high-biodiversity equilibrium, depending on the history of the system.
- Hysteresis. The system's response to changes in salinity will depend on its history. For instance, the wetland with initially high biodiversity and low salinity will switch to the low-biodiversity stable state at the collapse threshold as salinity increases. However, the wetland with initially low biodiversity and high salinity will not jump to the high-biodiversity stable state as salinity decreases back to the collapse threshold. Only when salinity decreases even further until the recovery threshold is reached, the wetland will be able to switch to the high-biodiversity stable state, provided that a species pool for recolonisation exists at the landscape scale.
- Initial state dependence. At an intermediate salinity level the wetland has two stable states of biodiversity. The stable state on which the wetland settles is determined not only by the environmental parameters, but also by its initial biodiversity state. There is also a threshold for biodiversity, corresponding to the unstable steady state, which is the dashed line in Fig. 3b. The wetland with an initial state of biodiversity above the threshold biodiversity will settle on the stable state of high biodiversity (the upper solid curve in Fig. 3b). The wetland with an initial state of biodiversity below the threshold biodiversity will settle on the stable state of low biodiversity (the lower solid curve in Fig. 3b).

We have also investigated another special case—namely how wetland biodiversity changes when salinity remains unchanged but other conditions vary.

4. IMPLICATIONS FOR MANAGEMENT

In addition to secondary salinisation, other wetland conditions (including water regime, climate, source of colonists and habitat heterogeneity and complexity) and biodiversity history have been recognised as potential drivers of biodiversity change (Davis et al. 2003). Here we have examined the theoretical relationships between some of these driving forces and biodiversity by exploring model dynamics. This set of drivers and their determinants leads to a corresponding set of management actions. The model guides the selection of measures that can assess biodiversity change. It specifies a single measure that has to show a clear response to salinisation and can include either structural (e.g., total number of taxa) or functional measures (e.g., productivity or decomposition).

Thresholds for the driving factors constitute an important aspect of resilience or sensitivity of the system. Protection requires improving resilience and avoiding crossing thresholds. Restoration requires improving sensitivity and engineering or providing opportunities for systems to cross thresholds. Empirical data could provide a characterisation of the dynamics of wetland ecosystems. In particular, empirical evidence on thresholds might provide an "early warning

system" for identifying wetlands particularly vulnerable to salinisation.
Wetlands of type 1 are dynamical, fragile systems. They are sensitive to disturbance or perturbation. Salinity and other conditions are the only factors that influence the equilibrium biodiversity of type 1 wetlands. Thus the single management action of changing initial biodiversity state such as revegetation will not be effective. Decreasing salinity is only one of the ways to promote biodiversity. Another possible management method is to convert a wetland of type 1 into a wetland of type 2 by improving other conditions than salinity. Then one can use the management methods for type 2 wetlands to induce further desired changes.

Wetlands of type 2 are dynamically robust yet fragile systems. Interactions, connectedness and nonlinearity result in the self-organisation of a number of species. These ecosystems are stable and resilient over a wide range of conditions, such that modest disturbances and perturbations are absorbed without long-term effect. However, once the threshold for a driver is reached, the wetland will undergo a sudden and dramatic shift in biodiversity. All the factors—secondary salinisation, other wetland conditions, and the initial biodiversity state—can drive the change of the equilibrium biodiversity of type 2 wetlands. Thus, for the protection or restoration of type 2 wetlands, more options for management are available: (1) decreasing salinity, (2) improving other wetland conditions, and (3) some combination of both. In addition, improving the initial biodiversity state can be used to restore type 2 wetlands in the bistable range.

Our model suggests that degraded type 2 wetlands are likely to be in a persistent, resilient, alternative stable state, requiring a unique recovery pathway, which is different from the pathway that led to the original collapse. Hysteresis implies that the degraded wetland of type 2 may be difficult to restore. Improving other wetland conditions than salinity alone may not be able to promote the system to high-biodiversity stable state. It cannot return to high biodiversity state by solely decreasing salinity to the collapse threshold. Further decreasing salinity below the recovery threshold, which is lower than the collapse threshold, is needed to recover the wetland. The sequence of management actions is important for restoration. Since decreasing salinity and/or improving other conditions will decrease the threshold for the initial biodiversity state (see Fig. 3c), thereby increasing the sensitivity of the wetland to perturbation, the sequence of management actions of first decreasing salinity and/or improving other conditions and then perturbing the biodiversity state might be a cost-efficient way to restore degraded type 2 wetlands.

5. ACKNOWLEDGMENTS

This research was supported by multi-regional NAP funding (Project number 202167).

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