Vegetation recovery in inland wetlands: an Australian perspective

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May 2017



Arthur Rylah Institute for Environmental Research Technical Report Series Number 270





Environment, Land, Water and Planning

Acknowledgements

This project was funded by the Water and Catchments Group (WCG) of the Department of Environment, Land, Water and Planning, Victoria (DELWP). Tamara van Polanen Petel and Janet Holmes (WCG, DELWP), and Freya Thomas and Claire Moxham (Arthur Rylah Institute for Environmental Research, DELWP) are thanked for reviewing the draft and providing valuable feedback. David Meagher (Zymurgy Consulting) is thanked for editing the report.

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Citation

Roberts, J., Casanova, M.T., Morris, K. and Papas, P. (2017). Vegetation recovery in inland wetlands: an Australian perspective. Arthur Rylah Institute for Environmental Research. Technical Report Series No. 270. Department of Environment, Land, Water and Planning, Heidelberg, Victoria.

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Southern Cane Grass *Eragrostis infecunda* establishing on exposed bed of former Lake Mokoan, at Winton Wetlands in October 2016. (Dylan Osler, via Jane Roberts)

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ISSN 1835-3827 (print) ISSN 1835-3835 (pdf) ISBN 978-1-76047-597-0 (print) ISBN 978-1-76047-598-7 (pdf/online)

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Summary

Section 1: Introduction

This review is concerned with deliberate or planned change of vegetation from one state to another, a process that is here called recovery but which refers to activities such as restoration, rehabilitation and repair. The aim is to present a useful and accessible summary of ecological understanding about wetland vegetation recovery, as it relates to Australia. This is an essential step in the development of scientifically sound tools that will assist wetland practitioners to be more effective in restoring wetland vegetation.

Such a review is timely. Knowledge about the distribution and general ecology of wetland plant communities in inland Australia has advanced considerably over the last 35 years. However, wetlands are under threat: a compilation of findings from around Australia shows a nation-wide pattern of loss and degradation, with very few instances of wetlands being in good condition. The challenge for the future is how to protect the remaining wetlands, and how to restore and rehabilitate wetland plant communities. Scientific input is needed if restoration and rehabilitation are to be done effectively. Despite huge community efforts in on-ground works, there is very little documentation, and hence only localised transfer of experience. This review aims to compensate for this by making existing scientific knowledge more available to users.

The review is limited to the vegetation of natural inland wetlands, including woody and non-woody vegetation, but with an emphasis on non-woody vegetation. Four topics relevant to vegetation recovery are covered: success and recovery, theoretical under-pinning, the significance of current vegetation, and climate change.

Section 2: Success and recovery

If recovery is to be successful, there must be an understanding and an appreciation of what success means, and that past activities are opportunities for learning and improving practice. In Australia there has been little focus on measuring success in terms of outputs, but a lot of attention on measuring success in terms of inputs, reported as statistics of activities, effort and materials. Despite the very large number of projects, documentation has been minimal and few appraisals have been done.

However, this is beginning to change. The concept of success, once considered nebulous, is being teased out: different types of success are now recognised, such as compliance (meeting contractual targets), functional (providing ecosystem functions and processes), and landscape (contributing to regional-scale ecology). Options for increasing success by learning from scientific knowledge are distilling scientific knowledge into practical tools, detailed reviews of case studies, examination of failures, adaptive management, and targeted research. Selected options are described, using Australian examples where possible: the review covers just four topics (passive restoration, types of intervention, wetland characteristics, recovery rates).

Section 3: Theoretical underpinning

A conceptual framework is provided as a diagram that integrates current knowledge about factors that influence change in wetland vegetation, and hence that shape vegetation recovery. The framework is in the form of a coherent diagram of the factors and processes shaping vegetation recovery in inland wetlands. This framework differs from conventional representations of ecosystem influences on wetland vegetation in explicitly recognising:

- two spatial scales (wetland and landscape)
- three types of connections between these (movement pathways)
- · a temporal shift from current to future vegetation
- the vegetation that is currently present (noting that both landscape and site characteristics influence how vegetation develops).

The structure of the conceptual framework is described, with examples.

Development or progress towards an expected end-point is known as a recovery trajectory. It is sometimes assumed by restoration practitioners that arrival at the expected end-point is an inevitable consequence of management activities, but this is not always the case. Five possible recovery trajectories are recognised, and shown diagrammatically: rapid recovery, delayed recovery, stalled, cyclical, and rapid decline. The first two reach the endpoint, so they can be counted as successful: these are fairly stable, single equilibrium

endpoints. Stalled and cyclical trajectories are when the trajectory does not reach the expected endpoint, instead resulting in persistent non-equilibrium states. Rapid decline is another case of not reaching the expected endpoint, and instead moves away from it: this can have multiple equilibrium endpoints.

Section 4: The significance of current vegetation

Current vegetation, meaning the existing plants as well as the sediment and canopy seed banks, contributes to vegetation recovery by providing propagules as well as favourable micro-sites where plants can establish. However, the capacity to do this depends on these elements remaining healthy and vigorous, and can be compromised if the plants become stressed. Current vegetation can also hinder recovery by seedling establishment by space pre-emption. Perennial plants that form dense tussocks or that grow laterally by rhizomatous clonal growth are highly effective at excluding other species. If these plants are not part of the long-term vegetation objective, then they need to be controlled, stressed or eradicated.

Seed banks give a wetland resilience, allow plants to establish even if no living plants are present, and are recognised as an important part of vegetation recovery for their role in passive regeneration. The seed bank is not a static entity. Seed abundance increases as seeds are deposited, and decreases as seeds germinate, lose viability, are predated or decay. Seed diversity also changes through time. Because of natural biases concerning which species become part of the seed bank, there may be very little similarity between the species composition of the seed bank and the species present in the wetland.

Section 5: Climate change and vegetation recovery

Climate projections for Australia, based on down-scaled projections of the 5th Intergovernmental Panel on Climate Change (IPCC), are that nearly everywhere will be warmer with more extreme conditions (heat, rainfall, drought) and that the southern regions will be drier because of altered rainfall patterns and higher evapotranspiration.

Existing knowledge of wetland plants and wetland plant communities suggests that the effects could be profound, though it is not clear over what time-scale this could occur: species growth, species interactions, and life-cycles could all be affected, as well as processes that help to maintain populations such as dispersal, colonisation and recruitment; and there could be more opportunities for invasive species to grow. Many studies comment on the individualistic nature of species response. Plant assemblages of the future will be novel assemblages, being a mix of resistant and resilient species and invading species, with some species losses. The challenges for vegetation recovery are how to set objectives and while working with different contexts simultaneously.

Section 6: Concluding remarks

As envisaged, the literature review has facilitated the development of a set of guiding principles and a decision support tool (DST) that will assist wetland practitioners when planning a vegetation recovery project. The four principles are expanded on, and future needs noted. A first version of the DST has been drafted, and a User Guide is in preparation that will be available as a downloadable application for a portable device. Also described here are two options that will be useful when planning whether to rely on passive or active restoration, and a recent advisory guide to restoration in a changing climate.

Introduction

1.1 Purpose and scope of this review

1.1.1 Purpose

The aim of this review is to present a useful and accessible summary of ecological understanding about wetland vegetation recovery in the Australian context. To achieve this, current knowledge about the ecology, dynamics and resistance of wetland plant communities is summarised in the context of wetland recovery. This is an essential step in the development of scientifically sound tools (discussed in Section 2) to assist those interested in wetland recovery, broadly scientists, managers and community groups, to more effectively restore wetland vegetation.

The review is about wetland vegetation rather than wetlands or wetland biota, because of the paramount importance of vegetation in ecosystem functioning. It comprises four interconnected topics:

- restoration success and ways that ecological science can improve this (Section 2)
- theoretical basis for restoration of wetland vegetation (Section 3)
- wetland vegetation attributes relevant to restoration (Section 4)
- likely effects of climate change and implications for vegetation recovery (Section 5).

1.1.2 Scope

The review is about the vegetation of natural inland wetlands, meaning those wetlands that are not under any tidal influence and classified as palustrine and lacustrine under the ANAE aquatic ecosystems classification (Aquatic Ecosystems Task Group 2012). Wetland vegetation means both woody and nonwoody plants: this review emphasises the non-woody plants such as herbs, which are wonderfully diverse (Box 1).

In this review, recovery is an umbrella term that embraces restoration, rehabilitation and repair.

Box 1: Diversity of herbs in Australian wetlands

Mudflat species: Plants (mostly herbs) that germinate and grow on wet muds exposed by falling water levels. Sometimes forming extensive mono-specific, even-aged swards. **Examples:** *Glycyrrhiza acanthocarpa, Ammania multiflora, Xanthium spinosum, Limnophila brownii*

Emergent: Plants that are rooted firmly in substrate, with the stem (or culm or shoot) growing through water into air; flowering and pollination occurs in air. **Examples:** *Eleocharis sphacelata, Phragmites australis, Monochoria cyanea, Persicaria orientalis*

Floating-leaved: Plants with roots in substrate, small and not robust; stem is either submerged and flexible, or floats on the water surface; flowering and pollination occur above the water, in air. **Examples:** *Potamogeton tricarinatus, Ludwigia peploides, Nymphoides crenata, Nelumbo nucifera*

Free-floating: Plants that float, on or in the water, and have very fine roots underneath: no stem evident. **Examples:** *Azolla filiculoides, Salvinia molesta, Ricciocarpus natans*

Submerged: Plants that grow while under water, and have most or all of their leaves submerged (some have a rosette at the water surface); their roots are fine and short; flowering and pollination occur at or above the water surface, except for charophytes. **Examples:** *Vallisneria australis, Myriophyllum verrucosum, charophytes, Potamogeton crispus, Lepilaena biloculari, Najas tenuifolia, Utricularia gibba*

Tussock-forming: Plants, typically grasses, sedges and some rushes, that grow in dense tufts or tussocks. **Examples:** *Paspalidium jubiflorum, Cyperus exaltatus*

Stoloniferous: Plants that extend laterally by above-ground stolons, and establish daughter plants distant from the mother plant. **Examples:** *Eragrostis infecunda, Cynodon dactylon, Vallisneria australis*

Clonal rhizomatous: plants with rhizomes, that extend underground, and emerge as shoots; often forming dense, mono-specific stands. **Examples:** *Baumea arthrophylla, Phragmites australis, Juncus ingens, Typha domingensis*

1.2 Knowledge of vegetation of inland wetlands

Knowledge about wetland plant communities in Australia has advanced considerably in the 35 years since the publication of *The vegetation of Australia* (Beadle 1981) which was the first national description of wetland vegetation.

A number of publications now cover Australian wetland vegetation. This includes three editions of *Australian vegetation*, each with a fresh look at wetland vegetation (Briggs 1981, Brock 1994, and Catford et al. in press); state-based descriptions such as *A field guide to Victorian wetland Ecological Vegetation Classes* (DSE 2012) and *Ocean shores to desert dune* (Keith 2004); introductory chapters in guides and keys such as *Waterplants in Australia: a field guide* (Sainty and Jacobs 2003) and *Floodplain flora* (Cowie et al. 2000); regional surveys and descriptions, such as for the Pilbara bio-region (Lyons 2015); and a new national perspective *Vegetation of Australian Riverine Landscapes* (Capon et al. 2016). In addition, there are floristic descriptions for a range of wetland types, such as coastal floodplains (Finlayson 2005, Boon et al. 2016), springs (Fensham and Fairfax 2003, Coates and Tolsma 2012), inland floodplains and wetlands (Brock et al. 2006, Catford et al. *in press*, Roberts et al. 2016), bogs and fens (Wahren et al. 1999, Hunter et al. 2013), peatlands (Whinam et al. 2003), montane lakes and lagoons (Bell et al. 2008), salt lakes (Brock and Lane 1983), depression wetlands (Casanova and Powling 2014), and floodplain billabongs (Catford et al. 2011, Halford and Fensham 2015).

Some of the broad patterns of wetland vegetation across inland Australia are reasonably well understood. For example, the species composition of wetland plant communities is determined largely by the regional species pool, filtered by abiotic and biotic characteristics, with water regime and water quality being the most influential of these at the site-scale. Families that are usually well-represented in wetland plant communities are Poaceae, Asteraceae, Cyperaceae, Juncaceae and Myrtaceae, with Chenopodiaceae and Fabaceae being regionally important (Catford et al. in press). Many wetland plant species are widespread, some are cosmopolitan: endemism is high in some areas, such as spring wetlands of the Great Artesian Basin, and south-western Western Australia (Catford et al. in press). The biogeography and generic character of Australian wetland plant communities is beginning to be understood but is still to be written.

Similarly, the basic characteristics of the wetland environment are also well-appreciated. Most wetlands in Australia have a variable water regime (with springs and karst caves being the principal exceptions). Water regimes in wetlands (meaning variation in surface water) can range from those where water is retained but water levels fluctuate, to those where water dries up completely and refilling occurs episodically. This variability results in submerged, saturated, drying and dry zones within a wetland, as well as wet and dry phases for wetlands; these zones and phases provide conditions suitable for plants adapted to wet, drying and dry conditions. As a result, wetlands have terrestrial, aquatic, amphibious and mudflat specialists, and are particularly diverse in life-forms (Box 1).

Many factors influence the composition and abundance of wetland vegetation, and because of this it is common to separate out their relative importance using a nested hierarchy and to categorise the driving factors as abiotic and biotic. This draws out the importance of spatial and temporal scales of influence, and can be represented as a conceptual diagram (for example, in Catford et al. in press) or explicitly tabulated (for example, in Thoms et al. 2016). Such representations are valuable but it is challenging to include temporal dynamics or spatial relationships, or to represent feedback loops. Humans, through past and present activities and practices, also influence wetland vegetation, by modifying or changing abiotic and biotic drivers. Although authors agree broadly about what determines wetland vegetation, they differ in how to represent human influences. For example, the conceptual diagram of Catford et al. (in press) makes the role of humans in natural systems explicit by providing examples of anthropogenic influences such as land use, eutrophication, fire regime, pollution, water abstraction for abiotic effects, and hunting, harvesting and invasive species for biotic factors.

Despite these advances, there are still areas where contemporary ecological knowledge is weak. Most advances have been driven by management imperatives such as wastewater treatment, salinity and salinisation, eutrophication, river regulation and drought (Catford et al. in press). The result is a bias towards plant-environment (abiotic environment) relationships, supported by an appreciation of resilience especially through seedbank studies, but a weak understanding of plant-plant interactions, medium-term and long-term vegetation dynamics, population viability and genetic diversity (Catford et al. in press).

1.3 Loss and degradation of wetland vegetation

Worldwide, wetland losses have been huge. Estimates of 50% have been widely quoted but are without basis (Davidson 2014). A recent review of available information considered that losses since 1900 AD may

be as much as 64–71% (Davidson 2014), and to have occurred faster in inland areas than coastal regions. In Japan, wetland area has decreased by about 60% since 1868 (Nakamura et al. 2006). Wetlands can be lost for a number of reasons, including natural events such as landslides, hurricanes, earthquakes, catastrophic floods or storms, but there is an acceptance that anthropogenic factors are the principal causes. A study of 105 cases of wetland loss in various parts of the world found that the most frequently cited proximate causes were reclamation for arable land and urban development, with economic growth and population growth being the drivers (van Asselen et al. 2013).

The situation in the Australasian region is similar. In New Zealand, 90% of the wetland area is thought to have been lost since European settlement (Ausseil et al. 2011). Loss statistics have not been compiled systematically for Australia, but from those available it is clear that losses have been extensive in some regions (Figure 1). It is also clear, from incidental studies and from regional and state reporting, that many of the remaining wetlands are in poor condition, particularly in the southern, more densely populated, areas. The examples shown in Figure 1 show the geographical extent of wetland losses, the range in condition, and the variety of causes.

Wetland losses and poor condition are strong indirect evidence that the state of wetland vegetation is also probably poor. This is not so well-known because the status and condition of wetland plant communities is rarely reported in Australia, as elsewhere. An exception is the inclusion of wetland vegetation in assessments of wetland condition, as in the Index of Wetland Condition used in Victoria (DSE 2005).

Examples of reports or observations on condition and status of wetland plant communities in Australia are:

- 35% of 1800 wetlands in Victoria assessed between 2009 and 2015 had wetland vegetation in poor or very
 poor condition. In 26% of wetlands, at least one wetland plant community (Ecological Vegetation Class or
 EVC) had >50% weed cover, and in 20% of wetlands at least one EVC was structurally modified, with less
 than half of the life forms expected to be present (DELWP 2016b).
- Various lines of evidence show that submerged macrophytes are in decline in riverine wetlands throughout the southern Murray–Darling Basin, but the extent of this loss cannot be quantified because of a lack of historical documentation (Reid et al. 2016, Catford et al. in press).
- 75% of *Typha* spp. and water couch (*Paspalum distichum*) grassland was lost between 1997 and 2007 in the northern nature reserve of the Macquarie Marshes in New South Wales (Bowen and Simpson 2008).
- 75% of the water couch/spike rush (*Eleocharis* spp.) association and more than 50% of the marsh clubrush association (*Bolboschoenus* spp.) was lost in the Gwydir wetlands of northern NSW between 1997 and 2007 (Bowen et al. 2008, Bowen and Simpson 2009).

Wetland vegetation loss and decline has negative consequences for the conservation of many species, including birds and amphibians listed as endangered or vulnerable at the national or state level. The challenge is to maintain the extant wetland plant communities through a two-fold strategy of protecting remaining wetlands, and restoring and rehabilitating. Given the extent of wetland losses to date, restoration and rehabilitation need to be as effective and successful as possible.

Restoring and rehabilitating wetlands has benefits beyond the wetlands because of the important ecosystem services they provide. For example, it is because of their role in maintaining a healthy landscape that an ambitious idea of restoring riverine wetland through the Mississippi Basin has been proposed (Mitsch and Day 2006). It is anticipated that wetland nutrient interception could drastically reduce nitrate-nitrogen load coming off agricultural land in the Mississippi–Ohio–Missouri River Basin, an enormous area which occupies 40% of continental United States of America, and that this would reduce the recurrent problem of an enormous hypoxic zone (20,000 km²) downstream in the Gulf of Mexico attributed to the use of nitrogenous fertiliser (Mitsch and Day 2006).



Figure 1: Wetland loss and degradation.

Key: Red call-outs are losses; green call-outs are condition. References for call-outs, starting top-left are: [a] EPA (2007), [b] Desert Knowledge CRC (2007), [c] Fensham and Fairfax (2003), [d] DEHP (2016), [e] Halford and Fensham (2015), [f] Bell et al. (2008), [g] Hunter (2013), [h] DEC (2006), [i] Carey and Macdonald (2008), [j] DELWP (2016a), [k] DELWP (2016b), [l] DPIW (2008), [m] Cunningham et al. (2011), [n] Casanova and Casanova (2016), [o] Pressey (1986), [p] State of the Environment (2011), [q] Balla (1994).

1.4 Wetland recovery

1.4.1 Recovery

Recovery as used here refers to a deliberate or planned change in an ecosystem from its current state to another 'improved' or 'better' state. It includes a range of human activities such as restoration, rehabilitation and repair. As an umbrella term, it embraces the various meanings of restoration and rehabilitation, words that are not used consistently in contemporary writing. Sometimes they are interchangeable and indistinguishable (e.g. Boulton et al. 2014) and sometimes are defined differently (e.g. Brierley and Fryirs 2008). The meaning of restoration, in particular, has shifted with time. For example, the *Primer* developed by the Society for Ecological Restoration interpreted restoration to be a process and an activity rather than an endpoint (SERIS & PWG 2004), whereas the recently published *National standards for the practice of ecological restoration articulated* by the Society for Ecological Restoration stere Group SERA 2016) adopted the process-based definition of restoration articulated by the Society for Ecological restoration is the process of assisting the recovery of an ecosystem that has been degraded, damaged or destroyed'. In contrast, rehabilitation is re-instating functionality to an ecosystem where restoration is not the goal.

1.4.2 Recovery reporting in Australia

In Australia, wetland recovery has been driven largely by a grass roots movement, as in other countries such as Japan (Nakamura et al. 2006). Community effort and involvement has been enormous and has been happening at least since the mid 1980s. This is evident from the activities of not-for-profit organisations such as Wetland Care Australia (NSW and South Australia) and Nature Glenelg Trust (Victoria and South Australia), and through the pages of *Wetlands Australia*, a newsletter published by the Australian Government since March 1995. This community effort is recorded almost entirely in the 'grey' literature and more recently on websites. There are very few accounts of wetland rehabilitation in the scientific literature (e.g. Finlayson et al. 1997), and even fewer of wetland vegetation recovery. Instead, the scientific literature focuses on technical developments, comparisons of techniques (e.g. Raulings et al. 2007, Robertson and McGee 2003), or advice on the implications for vegetation recovery. Descriptions of case histories, appraisals of rehabilitation, and even attempts to understand success or failure are exceedingly rare (Streever 1997, de Jong 2000, Nias et al. 2003).

This lack of reporting has been a major impediment to learning and to improving how restoration is practised, but it is not the only one. Another is that having a grass roots basis means there has been a local focus, which has made knowledge-sharing a challenge, at least in the era prior to the internet (McDonald and Williams 2009). A third has been the historical perception of what constitutes 'success'. It has been common for success to be equated with achievement, and for achievement to be measured in terms of human effort, materials, and resources expended. In contrast, *ecological success* (meaning that an ecological objective has been achieved, such as a wetland has recovered or a plant community has been restored) has been rarely mentioned, even though its ecological condition would have been the reason for activities and interventions. Failures have been forgotten, rather than being treated as opportunities to learn.

These patterns are evident in the pages of *Wetlands Australia*, which has profiled wetland recovery projects over two decades, making it a valuable archive. Its pages feature various activities, the diversity of support systems and how this has shifted through time, the very high level of volunteerism, and the range of funding programs and government initiatives. Sometimes the level of activity and commitment has been phenomenal, and makes for impressive statistics (Box 2). It is only in the last decade that the effectiveness of these efforts (predominantly threat abatement or removal activities) has begun to be questioned in the newsletter. Sometimes the questions are explicit, as in the case of an article on Lagoon Creek entitled 'Has the effort made a difference ?' (Barnett 2007), and sometimes not, as in the case of using traditional fire management to re-instate aquatic plant diversity following the removal of buffalo (McKaige 2009).

Wetland restoration is no longer solely a grass roots and community activity. State and federal governments, and major corporations, and community groups set up through specific state government initiatives, are all now involved in major or high profile wetland restoration programs. Many of these are to do with re-instating natural hydrology, or elements of the natural hydrology, such as the Basin Plan and the Living Murray initiative (Murray–Darling Basin Authority), the Lagoon of Islands project (Hydro-Tasmania), and Winton Wetlands in Victoria. In general such projects require major inputs and resources in the form of designed earthworks or infrastructure, or sophisticated modelling. A few are to do with remediating contaminated lands, such as Sydney Olympic Park in New South Wales.

1.4.3 Incorporating science

Ecological restoration of diverse ecosystems (including wetlands) has been happening for decades in Australia, at least since the 1930s¹. An overview of restoration activities (McDonald and Williams 2009) found that the 1980s and 1990s were characterised by high enthusiasm and a focus on on-ground works, that activities were often not effectively placed, and that there was an emphasis on removing the symptoms of degradation rather than addressing its underlying cause.

These characteristics were interpreted by McDonald and Williams (2009) as compelling evidence of the need to integrate science with practice. Several scientific disciplines were considered relevant to restoration notably landscape ecology, conservation biology, community ecology, resilience theory, restoration theory and reserves theory. The scientific perspectives they identified as being particularly relevant to effective restoration were understanding disturbance, resilience, and taking a longer-term view of vegetation dynamics.

McDonald and Williams (2009) identified two areas where bringing science and practice together would be expected to improve restoration and increase the likelihood of being successful. One was the need to develop a sound knowledge base about restoration by monitoring activities and projects effectively and then reporting on and evaluating them. The track record in this regard has been poor for wetlands in Australia. It was because of this poor track record that monitoring, evaluation and reporting was selected as one of eight criteria for identifying the 'Top 25' Australasian Restoration projects (all criteria given in Appendix 1) for show-casing on the website of the Global Restoration Network.

The other area McDonald and Williams (2009) identified was knowledge gaps. By this they meant topics and questions directly relevant to restoration, where either information or understanding was lacking. Their list of gaps was dominated by perspectives and processes that are hard to appreciate on the ground, such as corridors and connectivity, spatial and temporal dynamics, and the role of cryptic biota such as fungi. However, the most significant item on this list was not a knowledge gap but an issue to do with making science accessible and effective, viz: '*Transferability of scientific results between species (single to multiple) and regions.*'

¹ Global Restoration Network (GRN) http://www.globalrestorationnetwork.org/countries/australianew-zealand/ accessed 9th May 2016.

Success and recovery

2.1 What is success?

The concept of success is a nebulous part of restoration (Suding 2011) and has not been well understood. An example of this is shown in a survey of individuals involved in 69 wetland rehabilitation projects across Australia that commenced between 1969 and 1996 (Streever 1997). This survey found that:

- · rehabilitation covered both inland and coastal wetlands
- the size of the wetland being rehabilitated ranged from tiny to very large (from 0.4 to 110 000 ha)
- project duration varied enormously (from 1 to 28 years)
- · the principal cause of degradation ('impact') was altered hydrology
- · the most commonly stated goal was habitat restoration.

The survey also revealed that rehabilitation efforts were not always on target, as there were several projects doing activities such as planting or seeding that had no obvious link to threats described for that wetland. Significantly, the concept of success (i.e. rehabilitation success) was not deeply embedded in these projects, and was not clearly understood. Although respondents were clear as to what their goals were, there was an inability to offer any criteria for evaluating success: 'However, in response to a question about specific objectives that could be used to assess project success, respondents either reiterated goals or stated that no specific objectives had been developed.' (Streever 1997).

Uncertainty about what 'success' means in the context of wetland recovery has not been unique to Australia and was very evident also in the USA (Zedler 2007). In her review of 'success', based on two international journals dedicated to restoration science, Zedler (2007) found success was used in four ways: to predict outcomes, to judge outcomes, as criteria for judging projects, and to describe an ecosystem attribute. She noted a reporting bias towards *success* (used in the title, keywords or abstract of 116 articles between 2000 and 2006) and against *failure* (used in the title, keywords or abstract of only 10 articles over the same time-frame), and postulated that social pressures were responsible for this bias. Drawing on personal experience, she noted how the perception of success depended on perspective, goals and time-frame. In her example, which was the Friendship Marsh restoration project in Tijuana Estuary, the project was deemed a success (in the sense of completing the list of tasks and activities), even though the ecological outcomes did not eventuate as anticipated (although others presented themselves, resulting in ambiguous success), and some of the field experiments could be considered practical failures (yet these contributed to scientific progress).

Because it is an imprecise term (Kentula 2000), success needs to be defined at the start of a project. Advice on how to do this is clearly needed, but opportunities to do this are sometimes overlooked. The evaluation of success may be context-specific: ecological success may be evaluated using ecological measures, social success using social measures, and political or economic success using political or economic measures. Kentula (2000) proposed a three-way definition: *compliance* success for meeting the terms of an agreement or contract; *functional* success to evaluate ecological or ecosystem functions; and *landscape* success to evaluate the contribution to regional-scale ecology.

Ecological success (i.e. functional and landscape success) can be evaluated in different ways. One is to look at net improvement, which is the difference between degraded and restored sites. Another is to compare the outcome with expectations or objectives, or to evaluate how closely the restored site matches the reference description or the stated objectives, preferably using pre-determined criteria. This definition of success can be quantified, and even tested statistically; for example, by using BACI type designs and a falsification approach (Chapman and Underwood 2000).

In the case of vegetation, evaluating success needs to be done with a thorough knowledge of the processes that influence plant communities as well as what the goal of the project is. An example of this is species composition. This can be used as a specific goal but it is a very precise and stringent measure that can be hard to meet. Because of this, it is probably most sensible to use it in projects where it forms a major component of conservation goal, such as the restoration of *Sclerostegia* and *Halosarcia* communities in saltmarshes for Orange-bellied Parrot food. For broadly-based goals, measures of structural characteristics, life form diversity, productivity, and ecosystem services might be more relevant. Thus there is an art to choosing success criteria, and this complicates how success is evaluated. This point is visited again in section 2.2.3.

In addition, there is always potential for unexpected successes, as in the case of Lake Kasumigaura, the second largest lake in Japan (220 km², average water depth 4 m). The littoral zone had been heavily degraded by eutrophication, wave damage, and water level management, and the lake had lost 50% (by area) of emergent plants and almost all submerged macrophytes (Nakamura et al 2006). As part of restoration, an artificial littoral zone with a heterogeneous substrate was constructed, and inoculated with bottom sediments. The unexpected success was that, as well as meeting the stated objective of establishing a vegetated littoral zone, several macrophyte species appeared that had not been recorded for some time, including four species not recorded for over 20 years (Nakamura et al. 2006).

Unexpected results such as this might not be deemed a success in terms of achieving the stated objectives, but can be a powerful and emotive means of engaging public support.

2.2 Increasing success by learning

Around the world, the success rate of wetland restoration projects is poorly documented. The Wetlands Reserve Program in USA had three broad general objectives (recover hydrological function, wetland vegetation, and wildlife habitat) but the success of the program, at least in the south-eastern region, was not known until it was independently assessed some 11 years later (de Steven and Gramling 2013). The findings of this belated appraisal were generally positive, but this is not always the case. Mitsch and Wilson (1996) reported that one study found only a 50% success rate. An international overview of restoration projects did not give actual rates but affirmed that projects were not always successful, that evaluations were rarely comprehensive or rigorous, and that the scientific basis for much of the restoration effort was lacking (Suding 2011).

Project success can be increased in several ways:

- by distilling scientific knowledge and practical experience into a condensed and useable form or tool such as guiding principles, a decision tree, or specialist manuals such as for that produced for restoration in the Australian Alps (Good 2006)
- · through review and analyses of outcomes of case studies
- · by critical examination of failures
- by adopting an adaptive approach (Zedler 2005)
- by research, which can test assumptions under site-specific conditions, or trial techniques, all based on restoration theory.

Principles, reviews and analyses, failures and decision trees are discussed below. Scientific theory is discussed in Section 3.

2.2.1 Principles

Principles are a set of guiding statements that offer general advice on a matter. They may be based on experience or theory, or a combination of the two. Principles for wetland restoration and rehabilitation have been proposed by US EPA (2000), Zedler (2000) and Weinstein et al. (2001), and general restoration and rehabilitation principles have been developed by the Society for Ecological Restoration Australasia (Standards Reference Group SERA 2016). These are listed in Appendix 2.

The principles given by US EPA (2000), Weinstein et al. (2001) and Standards Reference Group SERA (2016) are pitched at the whole restoration–rehabilitation project, and consequently these have several themes in common: set clear goals, develop a project that is feasible, aim for an ecosystem that will be largely self-sustaining, be mindful of the landscape context, and use natural systems as a reference. The importance of monitoring as feedback and input to adaptive management is emphasised, and neatly stated by Weinstein et al. (2001): 'Principle 6: Site monitoring should be planned and implemented, and last until success is assured' (Weinstein et al. (2001). Only Weinstein et al. (2001) considered success: 'Principle 7: Success criteria should include functional as well as structured components'.

In contrast to the broad scope expressed in the principles in the three publications mentioned above, Zedler (2000) presented 10 principles as succinct messages that condense an area of scientific theory and ecological knowledge, and communicate this without theoretical detail. Although only some are specifically relevant to wetland plants (for example: 'Principle 7: Seed banks and dispersal can limit recovery of plant species richness'), all 10 are highly relevant for working with wetland plant communities.

Of all principles located in this literature search, Zedler's (2000) principles are the ones most relevant to recovery of wetland vegetation.

2.2.2 Reviews and analyses

Reviews and analyses of the effectiveness of wetland restoration are remarkably few. Most reviews originate in the USA and many of these cover wetland creation and mitigation, which is not relevant here. Meta-analyses, explained in Box 3, are the main type of review available, and these trawl the published papers, searching for examples and seeking to establish patterns or trends. Although they use case histories from around the world, the data set is biased by the large number of case histories from the USA. No comparable reviews or evaluations of wetland restoration success were found for Australia.

Because they use a relatively large sample size, reviews and meta-analyses can detect trends and influences that are not apparent from single studies. There is a tendency to simplify, however: restoration projects are condensed down to be a single datum point, thereby losing nuances and detail.

The findings of reviews and meta-analyses are summarised below for four selected themes:

- passive restoration (a single restoration technique)
- types of intervention (comparison of several techniques or practices)
- wetland characteristics
- · recovery rates and times.

Passive restoration

Passive restoration is the practice of relying on plants to self-establish by dispersal or from seedbank, without interventions such as planting or seeding. It is commonly used in wetlands after natural hydrology has been re-instated (such as removing barriers or filling ditches) or disturbance has ceased (such as the removal of livestock) or been reduced. It is also known as *natural regeneration* and has been referred to as *spontaneous revegetation*. Passive restoration is popular because it is a low-cost option. Background to passive regeneration is given in discussions of current vegetation (Sections 3.3.1 and 4.1).

Findings from passive restoration projects are summarised in Table 1 for six studies with quantifiable goals and one based on trends. Comparisons between restored and natural sites show progress towards the target (in this case, the target is the natural site condition), whereas comparisons between restored sites show whether progress is uniform, and can help to identify factors contributing to success. The studies cover a range of wetland types (isolated small wetlands, river flats, coastal saltmarshes) and study designs (replicated experiment, chronosequence), but are mostly for depressional wetlands. In all cases the natural hydrology was re-instated by plugging, in-filling or breaching, and in one study (depressional wetlands, South Carolina), invasive trees were removed. No examples of groundwater restoration or river flow restoration were located. Despite the enormous investment in hydrological rehabilitation of riverine wetlands in south-eastern Australia, no evaluations and no accounts of resulting ecological success have been published in the scientific literature.

The three principal themes emerging from the findings in Table 1 are as follows.

First, species composition of wetland vegetation did not fully re-establish from plants dispersing into wetlands, or from seedbanks: instead, species composition was a depauperate subset of reference vegetation.

Second, species and species characteristics were important. Certain guilds of plants (wet graminoids, native clonal perennials) generally failed to establish in depressional wetlands and prairie potholes. This was especially significant because it meant that supplementary activities would be needed to establish *Carex* sp., the dominant (and therefore characteristic) species in certain wetlands, which persists by vegetative growth and has low annual seed production (Galatowitsch and van der Valk 1996). Conversely, guilds comprising perennial competitive generalists (such as certain agricultural grasses) persisted despite hydrological change, and probably prevented native seedlings from establishing.

Third, dispersal limited recovery in coastal saltmarshes and small isolated wetlands in agricultural landscapes. The distance between potential propagule sources and the wetland being restored has been greatly increased by fragmentation and loss of intervening habitat. These distances were sometimes quite extreme, as much as 80 km for two coastal saltmarshes (Onaindia et al. 2001).

Table 1: Passive restoration.

Wetland type, location, and study	Comparison	Lapsed time*	Outcomes
DEPRESSIONAL WETLA	ANDS		
Prairie potholes Iowa, USA Galatowitsch and van der Valk (1996)	Restored vs natural (<i>n</i> = 10 pairs)	3 years	Species richness lower in restored wetlands (average 27 v average 46). Restored wetlands had fewer wet-prairie, sedge meadow, shallow emergent and floating annuals: had more submerged; had similar deep emergent perennials, mudflat annuals and woody species. Seedbanks in restored wetlands had fewer species 8 v 15 and were less abundant (3019 vs 7369 seeds per m ²).
Depression wetlands South Carolina, USA De Steven et al. (2010)	Before vs after (replicated treatments) (n = 16)	5 years	Species richness and composition similar to reference. Native clonal perennials did not colonise naturally.
Prairie potholes Iowa, USA Seablom and van der Valk (2003)	Restored v natural (<i>n</i> = 17, <i>n</i> = 10)	7 years	Total cover and species richness lower in restored wetlands. Species composition differed. Native perennials lacking from restored sites. Restored wetland flora was subset of natural, with few obligate wetland species. Floristic differences between restored and natural increases with elevation.
Prairie potholes lowa, Minnesota and Dakota USA Mulhouse and Galatowitsch (2003)	Contrasts and trends in vegetation attributes (species composition, richness) (n = 41 restored) Also considered results in Galatowitsch and van der Valk (1996) (see above) for 3 years after restoration	12 years	Similarity amongst restored wetlands increased through time (convergence) largely due to certain invasive perennials becoming abundant or dominant. Species richness increased. Species richness (max) inversely a function of isolation and flooding frequency. Certain guilds failed to establish (wet prairie, sedge meadow).
COASTAL SALT MARSH	IES		
Coastal saltmarsh Spain Onaindia et al. (2001)	Restored vs natural Restored vs restored	20 years 35 years	Species richness low in restored sites. Species composition not very similar to reference site.
Coastal saltmarsh England Garbutt and Wolters (2008)	Restored vs Natural (<i>n</i> = 18 paired sites) Chronosequence	2 to 107 years	Restored sites have fewer species. Estimated 137 years to reach species richness of reference site. Only 2 out of 18 sites matched reference for cover. Restored sites have higher cover of invasive perennial <i>Spartina</i> .
RIVERINE			
Valley-bottom wetlands Kwa-Zulu Natal, South Africa Cowden et al. (2014)	Before vs after (2 sites) Ecosystem integrity using reference metrics Ecosystem services	5 and 6 years	Better scores for ecosystem integrity at both sites. Increased scores for ecosystems services at both sites. Increase in obligate wetland species. Introduced grass resistant to change.

* Lapsed time means the time between restoration and assessment.

Types of Interventions

There are two broad approaches to vegetation restoration: *passive restoration* (as described above) and *active restoration*, meaning the deliberate introduction of plant material into a wetland, whether by planting or seeding. Active restoration includes *self-design*, described as 'the introduction of as many species as possible, knowing that natural forces will help in the ultimate design by choosing the most appropriate species. Self-design also recognises the importance of natural colonisation of species in wetland.' (Mitsch and Wilson 1996).

Passive and active restoration can appear to have differing outcomes, as shown by de Steven and Gramling (2013). They inspected 53 wetlands in South Carolina and Mississippi that had been restored 2–11 years previously under the Wetlands Reserve Program. They found that hydrology had been repaired using an array of techniques (ditch-plugging, tile-drain removal, installing water level controls, dikes), and had been largely successful (85–87%) when appraised against program aims, which were to 'recover hydrologic function, native wetland vegetation, and desired wildlife habitat' (de Steven and Gramling 2012, 2013). Wetland vegetation had been restored passively (following hydrological repair) or intensively (usually by planting trees). Floristic analyses found a persistent difference between these approaches, regardless of time since restoration. Wetlands that regenerated naturally were very similar to each other and to the natural wetlands in the region, whereas wetlands that were planted were more different, possibly because natural hydrological connectivity was not fully restored.

There are indications that the type of management intervention can influence success, regardless of whether success is defined as an improvement or as matching the natural condition. A meta-analysis of 70 experimental studies on wetlands (Meli et al. 2014) found that all types of restoration activity improved biodiversity and ecosystem services in restored wetlands relative to degraded wetlands, as indicated by mean response ratio being greater than 0 (left panel in Figure 2), but that the improvement was not always significant, as shown by confidence limits overlapping with zero. Management interventions generally succeeded in restoring biodiversity or ecosystem services to levels comparable to natural wetlands, as shown by confidence limits overlapping zero (right panel in Figure 2), the less-than-successful interventions being soil amendment, passive restoration and restoration of hydrological dynamics. According to this analysis, active revegetation, which is very much a community or volunteer activity, was slightly more successful than passive restoration.



Figure 2: Success of management interventions.

The effectiveness of 10 management interventions, including passive restoration and active revegetation, on biodiversity and ecosystem services in restored wetlands compared with degraded wetlands (left panel), and restored wetlands compared with natural wetlands (right panel). The diagram shows mean and confidence limits for response ratios, which compare Restored vs Degraded, and Restored vs Natural, with zero value indicating no difference for a measured attribute. [Taken from supplementary information for Meli et al. (2014).]

The value of active revegetation as a restoration activity was challenged in another meta-analysis by Moreno-Mateos et al. (2015), based on 628 created or restored wetlands compared with 499 natural ones. They compared the effectiveness of two restoration activities, re-establishing flow and surface modification, with and without revegetation. For nearly all the responses investigated, re-vegetation did not improve the

outcome relative to the restoration activity on its own, suggesting that passive regeneration achieved as much as active revegetation but was more economical in terms of resources and time. However, the application of these findings to recovery of natural wetlands is uncertain: the sample set uses both restored and created wetlands, and is strongly biased towards created wetlands.

Wetland characteristics

Recovery does not proceed smoothly or uniformly through time, and the overviews and meta-analyses showed that recovery rates vary with wetland characteristics such as size, type, and regional climate, but that the biggest influence on success was probably the cause of degradation (Meli et al. 2014).

Large wetlands (> 100 ha) recovered their biological components and biogeochemical functions sooner than smaller wetlands (Moreno-Mateos et al. 2012).

Wetland type affects the likelihood of success, with a higher likelihood in saltmarshes and rivers than in lakes, riparian zones and streams (Figure 3) (Meli et al. 2014). Wetland type also affects the rate of recovery. The analysis by Moreno-Mateos et al. (2012) found that biological components and biogeochemical processes of riverine wetlands were close to reference in just 5 years, whereas depressional wetlands showed very little improvement in biological structure over 45 years, and in biogeochemical processes over 25 years. The difference in recovery rates between riverine and depressional wetland was attributed to differences in hydrological connectivity and an assumed influx of materials, biota and propagules.



Figure 3: Wetland type and benefits of restoration.

The ameliorating effect of restoration activities varies with wetland type, as shown here for response ratios for ecosystem services. Each value is a mean, with standard errors. The dashed line at zero indicates the point where there is no difference between degraded and restored values: values greater than 0 indicate a beneficial effect. [Taken from supplementary information for Meli et al. (2014).]

Recovery was faster in warm climates: wetlands in cool climates progressed very slowly towards the reference state, showing little improvement in biological structure or biogeochemical processes in the first 15 and 50 years respectively. In contrast, the biological structure and biogeochemical processes of wetlands in temperate climates recovered in 5 and 30 years respectively (Moreno-Mateos et al. 2012).

Recovery rates and times

Recovery rates depend on which wetland attributes are being considered, whether hydrology, biological components or biogeochemical characteristics. Factors influencing recovery rate for biotic assemblages were similar – but not identical – to factors influencing biogeochemical function. Biotic assemblage structure is influenced significantly by the type of anthropogenic disturbance, the type of wetland and the regional climate, whereas the recovery of biogeochemical function is influenced by wetland type, regional climate and time. Animal assemblages recover faster and more completely than plant assemblages and soil organic carbon (Moreno-Mateos et al. 2015).

Time since intervention ('lapsed time' in Table 1) is an important consideration when assessing wetland recovery because processes recover at different rates. From a practical perspective, an understanding of this is essential if monitoring and evaluation are to be timed appropriately. For example, (Moreno-Mateos et al. 2012) found that a natural water regime could be re-established fairly quickly, but biological components reached only 77% of reference, even after 100 years, and biogeochemical characteristics reached only 74% of reference after 50–100 years.

Among the biological components, Moreno-Mateos et al. (2012) found that vertebrates took the least time to recover and plants the longest, and macro-invertebrates were intermediate. Specifically, vertebrate assemblages were similar to reference within 5 years (richness was slower than abundance); macro-invertebrates converged with reference in 5–10 years, although they did not become identical to reference, and plants took 30 years to approach reference but failed to become identical, even after 100 years.

With plants the response ratio remained consistently below reference, and this was attributed to dispersal limitation, sensitivity to imperfectly restored abiotic conditions, or possibly legacy effects.

2.2.3 Failures

Reasons for evaluating restoration activities and their outcomes are to test knowledge and improve it, to build support from the public and the scientific community, and to provide feedback on policy (Morandi et al. 2014). These reasons relate to successes as well as failures, yet failures are almost never evaluated. Only two papers were located that critically analysed failure, and these were on the same topic: the failure of biomanipulation as a restoration activity in shallow lakes (Sondergaard et al. 2007, Gulati et al. 2008).

The emphasis on success rather than failures is due partly to *publication bias* (the tendency to publish positive outcomes rather than negative ones), and partly to societal and political pressure. As a result, the literature on success is far larger than the literature on failures, and therefore estimates of success rates that are based on published studies should (in general) be treated with caution. For example, Suding (2011) summarised an earlier study based on 240 cases from a range of ecosystems, which found that 35% of the cases reported full recovery in 10–40 years, 35% had partial recovery, and 30% showed no recovery in any measured variable. The split between full, partial and no evidence of recovery is relevant to the 240 studies in the sample but publication bias against failures suggests these percentages are unlikely to be reliable estimates of actual trends. Publication bias can be avoided by careful compilation of the sample base; for example, by not relying solely on the scientific literature. Thus for their evaluation of river restoration in France, Morandi et al. (2014) compiled a database of 44 projects based on structured interviews rather than relying on publications.

Critical analysis of factors contributing to success and failure can be more useful than simply reporting success or failure. Morandi et al. (2014) documented not just whether a project had been successful or not, but also how success was measured (monitoring and evaluation), which they called *evaluation strategy*. This revealed the uncomfortable finding of an inverse relationship between the quality of the evaluation strategy and the degree of success: that is, a low-quality evaluation strategy was associated with successful outcomes, whereas a high-quality evaluation strategy (based on a BACI design) returned ambiguous findings about success. This demonstrates the challenge in designing an evaluation that is appropriate and also does not bias the outcome (Morandi et al. 2014).

Time since restoration needs to be considered when determining success and failure, because success is easier to determine with confidence than failure, and because recovery trajectories are variable, and can even fluctuate between apparent success and failure (Section 3.5). Response times vary between biota and between processes (Section 2.2.2) but are not understood well enough to be able to specify a critical period beyond which an activity can be deemed to have failed.

2.2.4 Decision support tools

In natural resources management, decision-making is usually guided by a framework based on scientifically robust techniques and procedures that are presented as a series of critical steps and lead to a particular decision or course of action. Decision-making frameworks are essential when making decisions about complex environmental problems, particularly those to do with water management as these typically mesh environmental and socio-economic issues, and are valuable for public communications.

Decision support tools (DSTs), also called decision support systems (DSSs), are computer-based information systems used to assist or guide decision-making. Often these are simulation models that can incorporate a range of physical and social complexities. They are commonly used to generate the outcomes from a set of decisions, and these outcomes or scenarios are used to inform decision-making. DSTs have been widely used in natural resources management in Australia, and are particularly evident in water and flow management, such as environmental watering (e.g. Gawne et al. 2012; Merrett et al. 2011). A large data library or an analogous form of information and knowledge is needed, covering at least ecology, hydrology, social matters and economics. Despite their very obvious power in combining a range of information and situations, there is some resistance or apprehension in using these, and their uptake is less than has been hoped (Watts and Butcher 2015).

Decision trees are DSTs that offer guidance on a specific matter, such as whether to progress with a particular management action. They are typically structured as a branching series of questions and answers; sometimes the answers are given as probabilities, in which case they are analogous to a technical appraisal. If they are based on quantitative data then the probabilities may be quantitative, such as 75% and 25% (e.g. Rout et al. 2013), but if they are based on qualitative information or expert opinion, then the probabilities will be qualitative or categorical, such as 'high' and 'low' (e.g. Oliver et al. 2012). The scientific strength lies in how questions are formulated. Their value lies in their simplicity (from the user's perspective).

No decision trees dealing with wetlands, wetland vegetation, or vegetation recovery were located. The example below (Figure 4) is about the capacity of fauna species to adapt to climate change (Oliver et al. 2012). The purpose is to establish the best or most sensible action to take. Adaptation is a large and complex matter, and in this case there were three decision trees, one for each of three situations: adversely sensitive areas, climate overlap areas, and new climate space areas. The decision tree for adversely sensitive areas (Figure 4) is relatively parsimonious, using just four questions. Because they provide such clear guidance, decision trees are invaluable as a way of condensing experience and understanding, and leading the user to a sensible decision.



Figure 4: Decision tree for a context-specific question on species adaptation (Oliver et al. (2011).

Box 2: Examples of large-scale efforts in wetland restoration in Australia

Revive Our Wetlands

Corporate–community partnership between Conservation Volunteers Australia (CVA) and BHP Billiton in a \$6 million partnership that has generated 'public awareness and interest in wetlands, resulting in unprecedented community action, minimised ecological impacts and a long-term conservation legacy' (Brittle 2010).

In ten years (2000–2010), the program delivered: at least 50 700 volunteer days; planted 822 915 trees, collected 1728 kg seed, propagated 53 336 plants; removed 4362 hectares of weed, cleared 41 929 kg rubbish, and built/maintained 220 km fencing: plus completed 366 flora and fauna surveys.

Wetland Care Australia (WCA)

Established in 1991 in South Australia, WCA pioneered wetland rehabilitation in the Murray–Darling Basin and is now the leading not-for-profit organisation involved in wetlands in Australia.

In its first 20 years it: it completed 360 field days, workshops and training days with 12 500 participants; partnered with at least 25 government agencies and 20 non-government organisations: planted 196 000 trees; conducted weed control on 5500 hectares; and completed on-ground works over 111 000 ha. WCA established best practice in areas of rehabilitation (Hajenko and Heyward 2011).

Box 3: Meta-analysis

Meta-analysis is the statistical analysis of results from multiple studies, taken from peer-reviewed literature. It is widely used to synthesise disparate studies, reveal trends and patterns, or resolve paradoxes.

The standard procedure is to calculate an *effect size*, also known as a *response ratio*, for a number of attributes such as species richness or soil organic carbon; then use these as data in a regression analysis such as linear mixed effects model, to determine the significance of factors of interest.

Meta-analysis has been increasingly used in ecology, and in evaluating restoration generally; partly because of its capacity to address questions at a wider scale than can be easily done with individual studies, and partly because it is so effective at reducing complexity. However, findings are constrained by the studies included in the sample, and by the fact that effect sizes are not independent if one set of results is used to calculate multiple effects (unless the analysts take particular care in this regard). For this reason, meta-analyses should be treated as indicative analyses rather than robust generalisations, especially as causality is not established.

An additional caveat in the case of wetland restoration is that results for created wetlands are sometimes included in analyses, in which case they are less likely to be relevant to the recovery of natural wetlands.

Theoretical underpinning for vegetation recovery

3.1 A conceptual framework

The conceptual framework presented in Figure 5 integrates current views on processes that influence plant assemblages and that drive change, and does this from a wetland perspective. This understanding has considerable value to practitioners aiming to recover wetland vegetation, because each of these processes provides insights into potential constraints on vegetation recovery, the likelihood of recovery without intervention, and the levers that can be used to steer restoration and accelerate the recovery process, as well as the spatial scale at which management needs to be applied.

This conceptual framework recognises two spatial scales: the wetland itself ('wetland context' in Figure 5) and the landscape within which the wetland sits ('landscape context' in Figure 5). At the wetland scale, abiotic and biotic conditions act as filters to determine the suite of species in the current vegetation that are favoured and persist over time to form the future vegetation. These processes are in turn influenced by the wetland's landscape context and the level of connection that the wetland has with it.

Landscape context represents the climate, land use, geomorphology, aquatic habitat and regional species pool of the landscape within which the wetland sits. Landscape context affects vegetation recovery as it influences the abiotic and biotic drivers of vegetation change within the wetland and the arrival of vegetation from outside the wetland. The influence of landscape context on vegetation recovery will depend on the extent to which the wetland is connected biologically and physically to the broader landscape. These connections are represented by three movement pathways that transport materials and organisms from the landscape to the wetland: water, biotic and atmosphere. Materials and organisms may move through more than one pathway.



Figure 5: Conceptual framework of processes that influence vegetation recovery in wetlands.

The water pathway represents surface, stream or groundwater flows to the wetland, and rainfall. Water pathways carry not only water to the wetland but energy, organic matter, nutrients, sediments, toxicants and organisms. The biota pathway represents the movement of fauna, such as turtles, waterbirds, fish and invertebrates, from places in the landscape to the wetland either by land, water or air. The biota pathway also transports nutrients, toxicants and energy that are consumed when animals forage in the landscape and then excrete wastes or die in the wetland. Similarly, seeds, dormant egg stages and parasites that are ingested or attached to an animal outside the wetland are subsequently transported to the wetland where they are excreted or detached. The atmosphere pathway represents the movement of sediment, water, toxicants, energy and organisms though the air via wind, thermal currents or volatilisation. The interplay of these three pathways on current vegetation influence the arrival of vegetation and the nature of abiotic and biotic interactions that shape the future vegetation (right-hand panel in Figure 5).

In this framework, unlike that discussed in Section 1.2, human influence is not treated as a separate process. Instead the framework recognises that all the pathways, processes and attributes are subject to change and modification, including by humans. Wetland Context and Landscape Context are described below, and Current Vegetation is described in Section 4.

3.3 Wetland context

3.3.1 Current vegetation

The ability of wetland vegetation to recover following a disturbance depends on how the vegetation and propagule bank have persisted in the wetland, what vegetation has arrived through dispersal or been planted, and how it responds to the current physical (abiotic) and biological (biotic) conditions in the wetland. This is explored further in Section 4. Abiotic and biotic conditions in the wetland drive changes in the vegetation by favouring some species while disadvantaging or eliminating others (Connell and Slatyer 1977, van der Valk 1981, Lortie et al. 2004).

The differential responses of species to the abiotic and biotic conditions depends on the attributes of the species and propagule bank present. Species attributes identified in the conceptual framework (Figure 5) are: life history strategy, water regime requirements for each life history stage, niche specialisation, physiological and morphological adaptation, and genetic diversity. Attributes of the propagule bank are propagule longevity and germination requirements (Figure 5).

In his wetland sieve model, van der Valk (1981) proposed that key plant life history traits could predict the persistence of wetland vegetation under different environmental conditions. Important life history traits used in this model included: life span, propagule establishment requirements and propagule longevity. In this model, life span considers whether the species present in the wetland are annual, perennial, or perennial with vegetation growth (which is treated as having an indeterminate life span). Propagules are treated as being long-lived if they produce a seed bank. Establishment requirements refer to water regime and differentiate species that germinate under flooded conditions from those that require a draw down to establish. Collectively these traits assess whether a particular species will persist under different water regimes as adults or in the soil seedbank, or whether they will be eliminated. Knowing these traits will help when planning the recovery of a particular species.

Similarly, knowing the types of plants present and how they respond to resource availability and disturbance can also help when planning recovery, as this can indicate likely problems. The C-S-R plant strategies identified by Grime (1977) are an example of this. Each strategy encompasses a trade-off in resources allocated to growth, reproduction and maintenance. Plants with a competitive strategy (C) tend to be tall and have high growth rates that enable them to monopolise resources: they are favoured under productive and stable environments. Examples are Typha spp., which are emergent wetland plants, and Phalaris spp., which are pasture grasses. Stress-tolerant plants (S) are favoured in low-resource environments, and have slow growth rates and conserve captured resources by having low rates of leaf turnover. Examples are Baumea spp. and Gahnia spp. Ruderal plants (R) have fast growth rates, short life spans and high rates of seed production: they are favoured in productive but frequently disturbed environments and are represented in wetlands by many aquatic herbs.

In aquatic environments, species vary in their morphological and physiological adaptations to submergence, waterlogging and drawdown, and this influences species persistence. The diversity of wetland plants is impressive and accounting for specific individual requirements of all species is rarely realistic. The development of wetland plant functional groups (Brock and Casanova 1997, Casanova 2011) provides a framework for predicting persistence based on water regime, making it a useful tool for recovery planning and setting objectives, as it avoids the need for precise species-level information.

The genetic make-up of the species that arrive in the wetland or that are introduced as part of the restoration can influence the vegetation assemblage that develops. If local adaptation has occurred then the local gene pools might perform better than those from other locations. However, the benefits of local adaptation need to be evaluated against the benefits of enhanced resilience to change that a more diverse gene pool offers. This is particularly important in the face of climate change, where the ability to re-establish or maintain historic environmental conditions may be compromised.

3.3.2 Biotic interactions

Changes in plant assemblages result not only from the selective pressure produced by the abiotic conditions (Section 3.3.3) of the wetland but through interactions with other organisms (Connell and Slatyer 1997). The Conceptual Framework (Figure 5) recognises three types of biotic interactions: plant-plant interactions such as competition and facilitation; plant-animal interactions such as herbivory; and plant-microbe interactions. Changes in communities that result from biotic interactions are referred to as autogenic.

Plant-plant interactions

Negative interactions among plants occur when plants compete for resources including light, nutrients, space, water and/or pollinators. Negative interactions occur when plants suppress the growth of other plants. Plants can inhibit the growth of other plants when they produce organic chemicals called allelochemicals that are released through volatilisation from their surfaces, leaf leachate or root exudate (Einhellig 1995). Plant allelochemicals usually inhibit germination or growth of other plants but can sometimes exert a beneficial effect on some plants (Einhellig 1995). Plants can also inhibit the growth of other plants when they produce high litter loads as this can suppresses germination and early establishment (van der Valk 1986, Carson and Peterson 1990). For example, invasion of restoration sites by Phalaris reduces light and increases litter production, which favours Phalaris dominance (Mathews and Spyreas 2010).

Positive interactions occur when plants facilitate the establishment of other species by providing protection from herbivory or unfavourable climatic conditions, or by providing resources. Plants that provide benefits to another plant are referred to as nurse plants (Connell and Slayter 1977, Ren et al. 2008). Plants can gain protection from unfavourable climatic conditions or herbivory by growing among 'nurse' plants that are adapted to these conditions. For example, established reed beds can act as nurse plants and facilitate the establishment of the wetland shrub Melaleuca ericifolia by protecting young seedlings that are highly susceptible to wind and wave activity (Raulings et al. 2007, Morris et al. 2008). Plants can also enhance the growth of other plants when they facilitate the acquisition of nutrients through the leaching of leaf litter. Deep-rooted plants are able to transfer water from deep soil layers to the upper soil in a process known as hydraulic lift, which can allow shallow-rooted plants to persist during dry conditions (Caldwell et al. 1998). Facilitation alters local conditions that other plants experience and effectively expands the area of suitable habitat that species can exploit.

Plant-animal interactions

Animals can influence plant assemblage in several ways: (i) through grazing impacts, (ii) when the effects of predators cascade down food webs to impact plants and (iii) when animals disperse plants and increase the likelihood of species colonisation or recolonisation.

Grazing animals influence wetland plant assemblage directly through trampling of vegetation, herbivory and the transport of plant propagules. They also influence plant assemblages indirectly by changing abiotic conditions including soil properties and water quality. Although disturbances such as grazing can prevent the competitive exclusion of species in productive systems and favour more diverse communities, in unproductive systems growth is restricted by resource availability, and grazing can cause diversity to decline (Proulx and Mazunder 1998). Grazing studies carried out in the Gwydir wetlands of New South Wales suggest that this response is likely to hold true in wetlands: grazing increased diversity in the productive Marsh Club Rush (Bolboschoenus fluviatilis) community but decreased it in the low-productivity Warrego Summer Grass (Paspalidium jubiflorum) community (Berney 2010).

Plant-microbe interactions

Microbial assemblages in the soil or water column can influence plant assemblage when they affect nutrient cycling, are pathogenic to plants, form mutualist associations, or compete with plants for resources (Ehrenfeld et al. 2005, Wisz et al. 2013). Plants themselves influence the microbial community that accumulate in their root zones or in the water column, resulting in either positive or negative feedbacks (Callaway et al. 2004, Wisz et al. 2013).

Positive feedbacks occur when plants increase the abundance of soil microbes that then have beneficial effects on plants: examples are mycorrhizal fungi and nitrogen fixers. Negative feedback occurs when plants increase the abundance of microbes that exert detrimental effects on plants (Callaway et al. 2004, Wisz et al. 2013).

Where plants are able to reduce the abundance of microbes that exert detrimental effect on their growth compared with other species, they can gain dominance. The dominance of some invasive species has been attributed to differences in soil microbial communities associated with their roots. For example the rapid range expansion of the invasive Spotted Knapweed (Centaurea maculosa) in North America has been attributed to the ability of this species to reduce the abundance of detrimental microbes (Callaway et al. 2004). Feedbacks between plant species and soil microorganisms of early-colonising species can determine the subsequent dynamics of plant communities (Kardol et al. 2007).

Of particular significance in aquatic systems is the role plants play in regulating rates of nitrogen cycling that are mediated by soil microbes. Aquatic systems are characterised by anaerobic soils, which can limit the activity of aerobic bacteria responsible for nitrification (Reddy et al. 1989). Stands of some emergent plants such as Common Reed (Phragmites australis) and Cumbungi (Typha orientalis, Typha domingensis) can aerate the root zone by internal convective gas flow (Dacey 1981, Brix et al. 1992). Aeration of the root zone by plants favours nitrifying bacteria, increasing the availability of nitrate, which can influence the co-existence of plant species that differ in their preferences for nitrate and ammonium (Boudsocq et al. 2012).

Priority effects

The order of species arrival in a wetland can have profound effects on what species establish and hence on what plant assemblage develops. This is referred to as priority effects (Fukami 2015). For example, species with high resource requirements might not be able to establish until species that enhance access to these resources have established. Similarly, where species arrive and exploit available resources, other species that share similar requirements will be excluded (Connell and Slatyer 1997). Where priority effects occur they have significant implications for vegetation recovery because the sequence of plant removal (for example by felling, weeding or spraying) or plant introduction (for example by planting) will greatly influence success.

3.3.3 Abiotic conditions

Changes in communities resulting from abiotic conditions are referred to as allogenic changes. Of the nine abiotic factors in the conceptual framework (Figure 6) the most important for plant assemblages in wetlands are water regime, nutrients and salinity.

Water regime

Water regime describes the depth, duration, frequency, timing, rate and variability of wetting and drying cycles. A wetland water regime creates a spatial and temporal mosaic of hydrological habitat that wetland plants can exploit according to their tolerance and adaptations to wetting and drying. Not only do plant species differ in their preferences for these hydrologic habitats, but preferences often differ at each life history stage including dispersal, germination, early establishment, and adult and reproductive stages, and this can shape wetland plant assemblages (van der Valk 1981, Middleton 1999).

Nutrients

The nutrient content of natural wetlands is highly variable, from bogs that are naturally very low in nutrients to marshes that are fed by surface or groundwater inputs and have naturally higher levels of nutrients (Sorrell 2010). Many wetlands experience artificially high levels of nutrients from human impacts, which can profoundly alter the structure and composition of wetland vegetation. If nutrient levels are elevated, primary production increases, which in turn increases competition for light, favouring tall competitive species and reducing understorey diversity (Hautier et al. 2009). If high levels of nutrients occur in the water column, algal biomass increases and can lead to the loss of submerged species through shading (Scheffer et al. 2001). Increases in plant productivity in response to nutrients can in turn increase leaf litter loads and lead to lower levels of dissolved oxygen, which themselves drive changes in plant assemblages. For example, high litter loads inhibit the germination of some species, and varying levels of tolerance to low oxygen will favour some species over others.

Salinity

Salinity refers to the total amount of all salts (including but not only sodium chloride), present in the water or soil of a wetland (Peck 1983). Salinisation is a major threat to aquatic habitats throughout Australia (Hart et

al. 1991). Salinisation due to human disturbance (secondary salinisation) results mainly from the clearing of deep-rooted native vegetation, and the introduction of irrigated agriculture on poorly drained land, causing saline groundwater tables to rise. Elevated groundwater promotes the seepage of saline groundwater into wetlands and brings salts to the land surface, where they can be washed into wetlands (Peck et al. 1983). Because salinity is increased by evaporation and reduced by freshwater inputs, it can vary temporally and spatially within a wetland.

Salinisation affects the nature of wetlands plant communities by causing the loss of salt-sensitive species. In Australia, wetland surveys indicate that aquatic plant species more commonly associated with freshwater habitats tend to be absent when salinity exceeds 5.9 dS/m (4000 mg/L), but significant species losses start to occur at salinities as low as 1 dS/m (680 mg/L). Once salinities reach 14.7 dS/m (10 000 mg/L) only halophytic species survive (Brock 1981, Brock and Lane 1983, Brock and Shiel 1983, Smith et al. 2009). Tolerance to salinity varies with life stage: early life stages appear to be more sensitive than adult life stages (Ganf and Morris 2016). Temporal variation in salinity can therefore provide periods of lower salinity that allow more sensitive species to establish and may allow them to persist in the population.

3.4 Landscape context

Landscape context has an influence on species composition and diversity of a wetland plant community. This happens through three processes that are mediated by the movement pathways in the conceptual framework (Figure 5):

- arrival of new species from the regional species pool
- arrival of new genotypes from the regional species pool
- inputs of materials that influence abiotic conditions in the wetland.

At the landscape scale, climate, geomorphology, land use and species pools determine the amount and types of materials that are transported, including nutrients, salts, toxicants, sediment, detritus, water and organisms. The transport of these materials is mediated through atmospheric, hydrological or biological pathways (Figure 5). The availability and behaviour of these movement pathways determine the rate, frequency and types of materials and organisms that reach the wetland.

The arrival of transported material can have varying effects on recipient wetlands, depending on the type and amount of material arriving and the current quantity of the material in the wetland. For many chemicals (toxicants, nutrients, salts), exceeding certain concentrations will have detrimental effects on vegetation. Similarly, as rates of species immigration increases, so too does the likelihood of colonisation or recolonisation, which may have either positive or negative effects depending on the species that are transported.

Wetlands are strongly connected to the surrounding landscape and to other wetlands through surface water flow and are thus greatly influenced by the amount of propagules, nutrients, sediments, salts and pollutants carried in water. Wind is an import movement pathway for plant propagules that have adaptations for wind dispersal and can also transport sediments and sediment bound nutrients and pollutants (Larney et al. 1999). Animals, particularly waterbirds, transport invertebrate and plant propagules among wetlands and through their foraging movements can import and export nutrients from wetlands.

Different land uses including urban development, agriculture and forestry can strongly influence the amount and types of plant propagules and type of materials transported. Human modification of the landscape can represent an important source of degradation to wetlands. For example, decreases in forested land cover can result in dramatic increases in runoff and sediment and nutrient yields (Allan et al. 1997).

The level of connection the wetland has with the landscape (macroscale) is influenced by the nature of the land immediately surrounding the wetland (mesoscale) and the size of the wetland. Generally the greater the perimeter of the wetland relative to its total area the greater the influence of the broader landscape (Polis et al. 1997). The properties of the landscape at the mesoscale can mitigate or intensify broader landscape influences. In wetlands, a buffer of native vegetation around the perimeter of the wetland is important in filtering sediments, nutrients and pollutants and can mitigate macroscale landscape influences. For example, larger buffer widths reduce nutrient and sediments loads entering waterways. When sites have steep slopes or surrounding land uses that increase sediment or nutrient transport, wider buffers are needed (e.g. impervious surfaces, roads, development, agriculture (Castelle et al. 1994).

3.5 Recovery trajectories

The conceptual framework in Figure 5 describes the processes that influence vegetation recovery, but it does not examine the temporal aspects. This can be done using recovery trajectories. A recovery trajectory

is a description of how vegetation changes over time. It can be useful for describing how vegetation is progressing towards a specified endpoint, and hence whether a vegetation project is on track for being successful.

Vegetation restoration projects should establish a target vegetation state (or reference state) that the program is expecting to achieve. Data from restoration projects have demonstrated that vegetation progresses towards a target at different rates, and may or may not reach the target. Moreover, the target may or may not be stable (i.e. the target state persists despite disturbances). Vegetation states that are stable are also called equilibrium states. Stability can be demonstrated in two ways:

- if that state is altered by a disturbance and subsequently recovers to its original state
- if the state remains unaltered despite the disturbance.

Five types of trajectories are shown in Figure 6, illustrating different patterns of vegetation change that can occur. These are: rapid recovery, delayed recovery, stalled, cyclical, and rapid decline. Only the first two trajectories are successful (i.e. reach a stable target that meets the restoration objectives).

In **rapid recovery**, the vegetation moves rapidly from its initial state and becomes similar to the target state, and then remains similar to the target state. **Delayed recovery** follows a similar path to rapid recovery but takes longer. In **stalled decline**, the vegetation shows an initial change towards the target state but then plateaus. **Rapid decline** follows a similar path to stalled decline, but goes into a decline instead of plateauing. In **cyclical recovery** the vegetation oscillates between moving towards the target state and moving away from it.

Suding and Gross (2006) explain these recovery trajectories in terms of ecological processes. They propose three recovery models based on differences in the underlying mechanisms (shown in Figure 6):

- • single equilibrium endpoint
- multiple equilibrium states
- • persistent non-equilibrium.

These models are characterised by different patterns of vegetation change, stability and predictability. While the theoretical underpinnings differ between these three types of recovery models, in practice it can be difficult to distinguish between them because stability might not be reached for a long time (Suding and Gross 2006).



Time

Figure 6: Theoretical vegetation recovery trajectories.

3.5.1 Single equilibrium endpoint

Patterns of vegetation change that show progressive improvement over time to reach a target state that is self-sustaining are consistent with the Clementsian theory that plant communities progress through a series of developmental stages that end in a stable climax community (Clements 1916). This pattern of change has formed the basis of most restoration paradigms (Suding 2011). Stability is produced through strong internal regulation and feedback loops, including life history trade-offs, competition, or plant–animal interactions. Where these biotic and abiotic interactions are intact, restoration merely serves to accelerate recovery, allowing it to reach a stable state sooner (Suding and Gross 2006). Sometimes systems progress steadily towards a single stable state more slowly than other similar sites. Slower rates of recovery have been attributed to differences in abiotic conditions, depletion of seed banks, or lower rates of plant dispersal (Suding and Gross 2006, Suding 2011).

Complete and relatively rapid recovery (10–40 years) has been reported in about one third of 240 restoration projects examined across terrestrial and aquatic ecosystems (Jones and Schmitz 2009). Rapid recovery was observed in Oak depression wetlands in Ohio, which recovered to the reference state after only five years because of a seed bank legacy (Martin and Kirkman 2009).

3.5.2 Multiple equilibrium states

Multiple equilibrium states (MES) or alternative stable states predicts that ecological systems may have more than one equilibrium state, even under the same environmental conditions (Scheffer et al. 2001). In these systems, trajectories are characterised by a regime shift involving a rapid change to an alternative state in response to a relatively small change in environmental conditions. Where this occurs, recovery may progress to different but stable states despite the re-instatement of abiotic conditions. Theoretically, multiple stable states occur when self-regulatory feedback processes that maintain the stability of the system break down, and the system experiences a major shift in species composition and ecosystem processes that result in alternative states. New alternative states are then regulated by feedback mechanisms that differ from those that regulated the original state. Because the two states have different reinforcing processes, the conditions required to induce a shift in state will differ, depending on the direction of the change. This type of change is sometimes referred to as hysteresis (Scheffer et al. 2001).

Multiple equilibrium states can occur in shallow temperate lakes when increasing nutrient levels result in the rapid transition from clear water dominated by submerged plants to a turbid, phytoplankton-dominated state (Scheffer et al. 1993, 2001). The collapse of the clear water state occurs as increasing nutrient levels overwhelm the system's control of algae production, so that algae increase to a level that reduces light in the water column to below the threshold required by submerged plants (Silberstein et al. 1986, McDougal et al. 1997, Moss 1998). This results in the elimination of submerged plants and the dominance of algae. At this stage, simply lowering the nutrient levels will not result in the re-establishment of submerged plants.

In systems where the internal self-regulatory processes have been altered, the system will be set on a different trajectory. In this case management intervention will fail to shift the system back to its original state unless the disrupted biotic processes that regulated the original state, such as plant–soil feedback or dispersal, are addressed.

Since its development in the early 1970s, MES has become an influential concept in applied ecology. However, much of the evidence for the existence of MES has been demonstrated through non-manipulative experiments or indirect methods which do not provide conclusive evidence for their existence in natural systems (Schröder et al. 2005). Schröder et al. (2005) assessed evidence for MES from manipulative experiments carried out across different ecosystems. Based on a set of criteria needed to meet the assumptions of MES, they found evidence for MES in 13 of the 35 studies examined, 8 showed the absence of MES, and 14 were inconclusive, mostly because the experimental time frames were too short.

A more recent review by Capon et al. (2015) examined evidence for MES in freshwater ecosystems and concluded that there was little evidence for their existence, although shifts between a clear water state dominated by submerged plants to a turbid, phytoplankton-dominated state in temperate shallow lakes, as discussed above, were observed. They propose that MES may apply only in specific environmental settings, such as temperate shallow lakes.

3.5.3 Persistent non-equilibrium

In some systems recovery may become stalled at an intermediate state, or may oscillate between periods of improvement and decline (stalled and cyclical trajectories in Figure 6), so that recovery is unstable and unpredictable. This instability in recovery is thought to arise for a number of reasons:

- · intervals between environmental disturbance are less than the time required for recovery
- abiotic conditions are not fully restored and prevent some species from re-establishing
- · priority effects inhibit the establishment of species
- dispersal limitation caused by landscape degradation depletes propagule sources or disrupts dispersal pathways.

Unstable trajectories were observed in restored wetlands in the USA by Mathews and Spyreas (2010). In these restored wetlands, species composition initially progressed toward that of reference wetlands in the first 4 years following restoration, but then diverged away from reference wetlands over longer time frames (5–11 years), mainly because of invasive species recruitment. In temporary wetlands, recovery may show a pattern of persistent non-equilibrium as wetlands move through wetting and drying phases that favour recovery, and phases that stall recovery or cause a transient shift away from the target state. The frequency of wetting and drying phases, and the rate of vegetation recovery during favourable phases, will determine whether the target is eventually reached.

4 The significance of current vegetation

4.1 Recovery potential

The recovery potential of a degraded wetland determines whether passive restoration (Section 2.2.2) is feasible or not, making this an important consideration in recovery planning. Recovery potential is determined by the condition of plants present in the wetland, the availability of propagules (seeds, spores, tubers, bulbs, turions) already in the wetland, and that disperse into the wetland. The relative importance of these three components (plants, seed bank and propagules dispersing into the wetland) is specific to each wetland plant community, so it differs among wetlands. Changes to any of these, for example as a result fire, cropping or drainage within the wetland or adjacent landscape, can therefore affect recovery potential, as well as being an opportunity for non-native or invasive species to establish.

As described above (Section 3.1), wetland vegetation is affected by factors and processes operating at two spatial scales. One is the local scale, meaning within the wetland: this is the *wetland context* in the conceptual framework (Figure 5). The other is the more distant or landscape scale, referred to as the *landscape context* in the conceptual framework, and is connected to the wetland by movement pathways.

In the wetland context, it is the characteristics of the individual species (life history strategy, water regime requirements, physiological and genetic fitness) and the characteristics of the seed bank (size, diversity, longevity and requirements for germination and establishment) that largely determine the future vegetation and its composition, and hence determine the success of restoration activities. These two components, that is the plants present and the seedbank, are *current vegetation* in the conceptual framework (Figure 5).

The condition and composition of current vegetation are the result of the disturbance history to the wetland. Examples of major disturbances are excavation for water storage, cultivation, and rubbish dumping. The historical contingencies of such a disturbance (e.g. changed water-regime, changed soil conditions, introduction of contaminants) can continue to affect vegetation for many years after the disturbance has ceased. Within the wetland, the presence, condition, genetic fitness and type of plants present determine the contribution of seeds and propagules to the wetland. In turn, the seed bank characteristics (diversity, density, longevity) and processes (entry into dormancy, germination) influence the establishment of new plants in the wetland.

The vegetation surrounding a wetland, especially if it is tall woody vegetation, influences processes in the wetland, by providing shelter or microsites for establishment of other species (James et al. 2015), and by contributing seeds or vegetative propagules directly to the wetland (Jensen et al. 2008). The seeds of woody or long-lived herbaceous species are rarely present in seed banks (Middleton 2003, Holland et al. 2013, Greet 2016) and hence those species are generally dependent on being dispersed into the wetland (via vectors, wind or water) from nearby vegetation.

In the landscape context, land use can have major effects on recovery potential by altering the abiotic conditions within the wetland that drive vegetation change (Figure 5). Examples of this are changes to wetland hydrology through drainage, pondage or changes in tree cover (Klimkowska et al. 2010) as well as contributions of nutrients and pollutants via movement pathways (Cui et al. 2013). Small changes in catchment land use can affect the landscape-scale connectivity among wetlands (Baudry et al. 2003). The presence of woodland, and location of remnants and planted corridors can have significant effects on the likelihood that wetland restoration will be successful (Baudry et al. 2003).

The description above outlines processes that modify recovery potential, and emphasises the significance of current vegetation (meaning the vegetation present and the sediment seed bank) in vegetation recovery. The following sections explore this significance further, describing what influences this role and how variable it can be. There is a rich scientific literature on seed banks that is highly relevant to vegetation recovery but which has not as yet been synthesised. The various influences on current vegetation are summarised in a diagram (Figure 7). This shows the dynamics between four vegetation 'pools' found in all wetlands: seed bank, seedlings, soil carbon (as a surrogate for dead plants, litter), and living vegetation (in the wetland, nearby and in the catchment). Four processes cause a pool to transition from one to another: dispersal, dormancy breaking, germination and death.



Figure 7: A dynamic perspective of vegetation pools.

Vegetation pools in a wetland (blue-grey, green) and the processes (arrows, italics) that cause them to change from one pool to another, or to become soil organic carbon. 'Adjacent vegetation' means living vegetation in and around the wetland.

4.2 Wetland context — current vegetation

4.2.1 Local effects

Local land use (on adjacent land) can influence the structure and function of wetland vegetation, including seed banks. The effects include the impacts of farming and urbanisation (McCarty et al. 2009, Cui et al. 2013) and the presence and abundance of competitive or weed species (Hazelton et al. 2014). Negative effects can be ameliorated by the proximity of other wetlands (Lopez and Fennessy 2002) and areas of native vegetation (Alsfeld et al. 2010). Where the surrounding land use is cultivation and cropping, this can alter wetland hydrology by decreasing the amount of runoff that reaches a wetland (Elliot et al. 2001) or increasing sedimentation (Zartman et al. 2010). Cultivation and cropping can also influence site fertility (Swink and Wilhelm 1979) and provide direct and residual herbicide contamination (Elliot et al. 2001). Exotic pasture and crop species can invade wetlands. Where the surrounding land-use is urban the number of seedlings establishing from seed banks. Where the surrounding land-use is urban the number of

Vegetation that is near a wetland is likely to be a more effective contributor of propagules than vegetation that is further away. Seeds of trees and herbaceous species are dispersed over an area determined by plant height, seed weight and seed dispersal structures (Boomsma 1950, Nathan et al. 2011). Some perennial species, such as wetland trees (e.g. River Cooba, Black Box, River Red Gum) and long-lived shrubs (e.g. Lignum) have buoyant seeds that can be dispersed by water (Capon et al. 2009, Roberts and Marston 2011). If adult plants of such species are absent from a wetland, the arrival of seeds is driven by hydrological connectivity.

4.2.2 Vegetation condition

The condition of the long-lived herbaceous and woody species is relevant to vegetation recovery because reproductive effort is sensitive to condition. Some of these are serotinous (ie retain seed in canopy rather than form a seed bank) and poor condition reduces their capacity to contribute propagules. Condition is affected by water regime (stress from more permanent inundation or less frequent inundation), senescence (from age or disease), fire, salinity and land use (e.g. grazing).

In Australia, the importance of condition for reproductive processes has been established for dominant floodplain and riparian trees, such as *Eucalyptus camaldulensis, E. largiflorens, E. coolabah, Acacia stenophylla* and *Duma florulenta*, which also occur in wetlands. If the condition of these wetland *Eucalyptus* trees is poor (usually due to hydrological stress as a result of infrequent flooding) the result can be poor flowering, reduced fruit development (Jensen 2009), low seed set (George 2004, Jensen et al. 2007, 2008) and longer seed retention on the tree (George 2004).

The effect of stress and poor condition on the reproductive output of non-woody species is less often considered, but equally important. Heavily grazed stands of sedges and rushes can fail to produce flowers and seed altogether. At the site shown in Figure 8, *Gahnia filum* seeds did not germinate from the soil seed bank, so it is likely the presence of healthy, reproductive plants in or nearby is necessary for the expansion of the area occupied by *Gahnia filum* and subsequent restoration of the site.

The shoots of rhizomatous emergent macrophytes such as *Typha* spp. need to develop to a certain size in order to become reproductive: shoots that fail to reach the minimum height because of water stress, grazing or poor condition do not flower. In western New South Wales, the critical height for *Typha domingensis* is 900–1000 mm, and for *T. orientalis* it is 1700–1800 mm (Roberts 1987). Submerged freshwater plants can experience stress when saline water enters temporary freshwater wetlands. The responses of species differ, but although individual plants might germinate and establish in saline water, sexual and asexual reproduction can be reduced or prevented in susceptible species (James and Hart 1993).

4.2.3 Interactions among plants

Plant communities are not static, and plants can affect each other and influence recovery in a variety of ways, although only a few of these are much recognised. For example, Gómez-Apararicio (2009) reviewed interactions among plants in relation to restoration of degraded ecosystems and found that competitive interactions (among species) were the focus of many studies, but that lesser-known interactions (such as facilitation and neighbour effects) could also be important in determining restoration outcomes.



Figure 8: Heavily grazed stand of *Gahnia filum* along the Wannon River.

Priority (competitive exclusion from being there first)

Plants compete for resources (water and nutrients) and light, but vary in their competitive ability. Although vegetation can have a number of positive benefits in degraded ecosystems (shade, organic matter, amelioration of the effects of wave action), it can also prevent the establishment of new individuals by hindering germination, establishment or growth. Gómez-Apararicio (2009) found that herbaceous species were more likely to have a negative effect on the establishment and growth of neighbours or new vegetation than shrub or tree species, and this was particularly true for wetlands. Long-lived herbaceous species that produce a dense stand of tightly packed leaves and stems and expand by rhizomatous growth (e.g. *Typha domingensis, Phragmites australis, Phalaris aquatica*) are generally very effective at excluding other plants. If such species already occupy a wetland, they can prevent the establishment of other species. Their removal can assist recovery by allowing the establishment of other species, whether by germination from the seed bank, dispersal into the wetland, or planting (Minchinton et al. 2006, Hazelton et al. 2014).

Facilitation (providing opportunities for other plants)

Facilitation is the process whereby one plant assists the establishment, growth or survival of another. In his review, Gómez-Apararicio (2009) found that facilitation can be used as a restoration tool. On balance, the presence of vegetation was particularly important for the germination and establishment phases of emerging plant communities, but was less beneficial in later growth phases.

The role of facilitation in Australian wetlands is almost unknown, with only a very few studies on this topic. In one study, James et al. (2015) showed that the establishment of herbaceous plants was facilitated by Tangled Lignum, a dense woody shrub (*Duma florulenta*) of riverine wetlands, and in another, Good et al. (2014) found that seedlings of Coolibah (*Eucalyptus coolabah*) survived better when protected from frost by herbaceous plants, a process that helps to explain the dense thickets of Coolibah seedlings on northern NSW floodplains (Good 2012). Retention of woody vegetation, even if it is undesirable in the long-term, can facilitate the establishment of more desirable vegetation in the early stages of wetland recovery.

4.3 Characteristics of the seed bank

The sediment seed bank means the bank of living seeds, spores and specialised vegetative propagules (tubers, bulbs, turions) stored in the soil of wetlands. Tubers and bulbs are storage or reproductive structures produced by the roots of plants (tubers) or by contracted buds (bulbs) underground, and are typically produced when the plant is actively growing (Rea and Ganf 1994). Turions are the contracted apices of shoots in submerged plants (e.g. *Utricularia, Myriophyllum* and *Potamogeton*) that allow plants to over-winter in permanently wet habitats. Rhizomes and stolons are not included in the definition of the seed bank because they retain a connection to the parent plant. Although there is huge variation in the size of seeds in the plant world (from orchid seeds weighing just a few micrograms to coconuts weighing 1-2 kilograms), the majority of wetland plants have small seeds, usually less than 2 mm in diameter (Sainty and Jacobs 1981).

The sediment seed bank develops as a consequence of seeds arriving (dispersal in Figure 7) and remaining viable and dormant (i.e. not germinating immediately). Dormancy can be innate (or primary) dormancy, or enforced (or secondary) dormancy (Harper 1977). Innate dormancy is failure to germinate due to a mechanism imposed by its physiology (e.g. immaturity or a requirement for stratification) or its structure (e.g. hard seed coat). Enforced dormancy is failure to germinate due to a condition imposed upon the seed by its surroundings (e.g. inappropriate temperature, light, oxygen or moisture).

Seed banks convey resilience to wetland ecosystems by providing a mechanism for vegetation to reestablish after a disturbance (Brock and Rogers 1998, White and Stromberg 2011, Casanova 2015). Because of their role in vegetation persistence, especially in a variable climate, developing a viable and abundant seed bank is especially significant in ensuring vegetation recovery in the long-term. Germination from the seed bank is essential for successful wetland restoration in many parts of the world (e.g. Aponte et al. 2010, van der Valk et al. 1992, Brock and Britton 1994). Even if a plant species has been lost from the current vegetation, or has become locally extinct, it can sometimes be present in the seed bank (Keddy and Reznicek 1982, Faist et al. 2013). Seed banks in Australian wetlands are usually persistent, and propagules can remain dormant for years or decades (Brock 2011). In general, when a seed bank is diverse and abundant, the dryland phase of wetland seed banks, and the native wetland species, can germinate in response to the restoration of hydrology in disturbed systems (Eldridge and Lunt 2010).

The number of seeds in the seed bank can vary depending on processes such as dispersal, and germination (Figure 7), as well as the characteristics of the wetland. Estimates of seed bank density for Australian wetlands range from thousands to hundreds of thousands of propagules per square metre (Table 2).

Similarly, species diversity varies from being depauperate (fewer than 10 species) to highly diverse (30–200 species) (Table 2). However, caution is needed when comparing wetlands because estimates of abundance and diversity are highly dependent on the area sampled, the sampling method used and the method used to assess germination. Seed banks are usually assessed by exposing them to a germination stimulus, then identifying the species that establish. In the case of wetland seed banks, the stimulus is usually very shallow flooding. Shallow flooding of sediment samples is known as the emergence method (Poiani and Johnson 1988). There is also the possibility of a slight bias. Most seed bank studies provide conditions for short-lived herbaceous or graminoid species to germinate but rarely continue long enough to allow species with long-lag-times between stimulus and germination to be detected (cf. Finlayson et al. 1990, Casanova 2004).

Table 2: A comparison of Australian sediment seed banks.

Studies are grouped by type of wetland (bold capitals), and show where study took place and reference. Density is the average (x) or range of viable propagules in the soil (n = number of sites sampled). Diversity is the total number of species in the whole study. All studies used the emergence method.

FLOODPLAINS and FLOODPLAIN WETLANDS						
Northern New South Wales (Narran) (Webb et al. 2008)	20–90	12				
Inland New South Wales (Brock et al. 2006)	300–41,000	2–10 (per pot)				
Inland Queensland, Cooper Creek (Capon 2007)	2941 (<i>n</i> = 1)	36				
Tropical floodplain grasslands (Finlayson et al. 1990)	3800 – 15,400 (<i>n</i> = 3)	33 (<i>n</i> = 3)				
South Australia Murray River wetlands (Jensen et al. 2008)	2051 (<i>n</i> = 3)	16				
TEMPORARY NON-RIVERINE WETLANDS						
South east Queensland (Osunkoya et al. 2014)	3145 - 61,090	x = 26				
Cultivated wetlands (ricefields) (McIntyre 1985)	x = 177,000 (<i>n</i> = 9)	34 (<i>n</i> = 9)				
Southeast of South Australia (Bool Lagoon) (Nicol et al. 2003)	22,000-78,000	27				
Upper south-east of South Australia (Goodman et al. 2011)	<i>x</i> ⁻ = 1270	13 – 21				
Riverine Plains temporary wetlands (Eldridge and Lunt 2010)	x=26,333 (n = 9)	82 (<i>n</i> = 9)				
PERMANENT WETLANDS						
Western Victoria (Lake Fyans) (Casanova 2005)	<i>x</i> ⁻ = 163,060	6				
Northern inland Victoria (AWT 2000)	9677 – 33,531 (<i>n</i> = 5)	35 (<i>n</i> = 5)				
RIPARIAN						
Northern Victoria (Greet et al. 2012)	x = 5698 (n = 5)	115 (<i>n</i> = 5)				
Northern Victoria rivers (Greet et al. 2013)	x= 28,000	117				

4.3.1 Relationship between the seed bank and vegetation present

Although the seed bank is derived from the reproductive efforts of the vegetation present within and adjacent to the wetland, as well as the historical vegetation and distant vegetation that has dispersed into the wetland (Figure 7), the species diversity and representation in the wetland seed bank rarely mirrors the vegetation present (e.g. Hopfensberger 2007).

Partly, this is because the composition of the sediment seed bank is somewhat biased. For example, there are usually not many representatives of species whose reproduction is largely vegetative, or of serotinous species (seeds that are carried within the canopy), or of bird- or ant-dispersed seeds (Middleton et al. 2003, Casanova 2015). As a consequence there is usually low similarity between what germinates from the seed bank and the current vegetation (Raffeale 1996, Touzard et al. 2002; Beas et al. 2013; Casanova 2015). There are exceptions (e.g. Leck and Graveline 1979, Brock and Rogers 1998), such as wetlands exposed to frequent natural disturbances (as in tidal freshwater marshes), and wetlands where the vegetation is dominated by annual or short-lived species, such as in Australian rice fields (McIntyre 1985). The longer the time between natural disturbances, the less similarity there will be between current vegetation and the seed bank (Touzard et al. 2002). The likelihood of a mismatch between sediment seed bank and current vegetation means that natural regeneration could produce some surprises, and that expectations of what might emerge might need to be tested.

Species in the seed bank can have a similar water regime preference to the current vegetation. For example where the vegetation is dominated by species with an amphibious water regime requirement, the seed bank is likely have the same requirement (Brock 2011). There is rarely strong zonation in seed banks in relation to water-level at the time of collection (Casanova and Brock 1990, Brock and Rogers 1998, Casanova 2015); rather, the distribution of species in wetland sediment can be patchy, related to historical water-levels and plant occurrences (Bigwood and Inoye 1988).

In many cases dispersed propagules do not retain dormancy for long periods of time. Germination from the seed bank is likely to allow a proportion of the natural vegetation to establish, but is unlikely to result in the restoration of a community identical to an undisturbed site.

4.3.2 When is a seed bank abundant and diverse?

The quality of the seed bank, meaning its abundance and composition, is relevant in vegetation recovery if the recovery relies on passive restoration. It is quite possible for there to be too few propagules in a seed bank to ensure regeneration, even when other factors are manipulated to enhance establishment (Rodrigo et al. 2013). Knowing the circumstances that cause seed banks to become depauperate can help managers make better decisions about whether to rely on passive restoration or not.

Wetland seed banks vary enormously in the abundance of propagules and the diversity of species within them (Table 2). Some seed banks (and the vegetation that produces them) are less abundant and less diverse than others. Arctic, subarctic and north-eastern Chinese wetlands are particularly depauperate, with only a few hundreds of seeds m⁻² (Wang et al. 2013), whereas the seed banks of Australian temporary wetlands in temperate zones can have tens of thousands (Casanova and Brock 1990, Eldridge and Lunt 2010), or even hundreds of thousands of propagules per square metre (McIntyre 1985). As yet there is no analysis or study that has characterised the seed banks of Australian wetlands, but it is clear (Table 2) that they are usually in the range of thousands to tens of thousands of propagules per square metre, and that species diversity is highest in temporary, temperate and semi-arid, palustrine wetlands, and lower in alpine and heathy wetlands, with vascular species counts ranging from as low as seven per site (Finlayson et al. 1990) to 115 across five sites (Greet et al. 2012). High diversities are often a consequence of different suites of species occupying the wetland during different phases of the water regime (e.g. mudflat species during recession; submerged and emergent species during inundation), so wetlands with a permanent, stable water regime (i.e. few water-level fluctuations) can be expected to have a less diverse seed bank than temporary wetlands.

4.3.3 What depletes the seed bank?

Seed banks are naturally depleted by germination and replenished by plant reproduction and dispersal (Figure 7). They are finite: if not maintained by a continual or seasonal input of propagules, they can decline in both diversity and abundance (Zedler 2000, Brock 2011), and even become exhausted (Leck et al. 2012). The main factors that deplete seed banks are germination following disturbance, granivory, and grazing.

Long-term survival in seed banks (seed longevity) is a species characteristic. It is determined by initial seed quality, which is affected by genotype and pre-storage environment (Ellis and Roberts 1980), the resources stored within the seed (correlated to seed size and shape: Bekker et al. 1998), the temperature and moisture during storage (which can be correlated to depth of burial: Bekker et al. 1998) and the dormancy characteristics of the species. One European study established that longevity values range from 'transient' (< 1 year) for species of *Myriophyllum*, *Callitriche*, *Potamogeton*, *Ruppia* and *Utricularia*, to 'persistent' (> 1 year) for *Callitriche palustris* and *C. truncata* (Kleyer et al. 2008). By this definition, Australian wetland seed banks are generally persistent. Brock (2011) recorded the 'residual' survival (i.e. after annual germination events without replenishment) and 'longevity' (i.e. germination after storage without a germination stimulus)
of wetland plant seeds and found that the mean longevity was 7.4 years, and that the residual germination was still high (48% of initial germination) after 7 germination stimulus events in 7 years. The longest dormancy recorded for that study (which was reported after 12 years, but is ongoing, M.A. Brock pers. comm.) was 12 years (13 species). Although long, this is not exceptional. For example, in Chinese sedge meadows, seed banks have been found to persist in the presence of cultivation for longer than 15 years (Wang et al. 2013).

Species differences in longevity and viability will influence the floristic outcome. For example, Wang et al. (2015) found that key structural species can have short-lived seed banks (c. 6 months) and the abundance of many species declines in the first 1–5 years, becoming absent or rare after 10 years. It is likely that herbaceous species last longer in the seed bank than do woody species (Middleton et al. 2003). Some herbaceous species were still present in wetlands that had been farmed, with annual flooding, for 50 years (Middleton et al. 2003), and there is a record of charophyte oospore survival for at least 45 years in lake sediment (Rodrigo et al. 2007). These studies show that seed banks are naturally resistant to decline, but that time and treatment can cause species to be removed and abundance to be reduced. In general the seed bank of a wetland that has been disturbed for longer than about 5 years can be expected to have less diversity and abundance than the same wetland in an undisturbed state. There is thus a window in time when the seedbank will be a reliable tool in vegetation recovery; but beyond which it becomes more uncertain.

Water regime changes can also deplete a seed bank. The seed bank of temporary wetlands that become permanently flooded can continue to be a resource for restoration, but the length of time a seed bank can persist will depend on the environmental conditions (temperature, oxygen availability, soil and water chemistry), and the opportunities for replenishment that occur. Seed banks of temporary wetlands are likely to naturally decline over time when the wetland is permanently flooded (see seed bank longevity above). Similarly, seed banks of species whose seeds are intolerant of drought such as *Aponogeton distachyos* (Swidells 2002) are likely to decline under dry conditions. Water level manipulations that allow germination from the seed bank but do not allow plants to mature and reproduce are likely to markedly reduce the seed bank (de Winton et al. 2004).

Disturbance

Physical disturbance of a seed bank, such as cultivation, pugging and trampling, and excavation, is generally a stimulating event for the germination of propagules, and hence contributes to a reduction of the seed bank. Movement of the soil can expose propagules to light or temperature conditions that break dormancy (de Winton et al. 2004). Physical disturbance can stimulate mass germination (Smith 1998) or enhance germination from what appear to be depleted seed banks (Casanova 1994, Brock 2011). The effect of physical disturbance becomes complicated in cases where it is accompanied by other changes, such as cropping accompanied by biocide application or altered nutrient ratios (Qu et al. 2014). Long-term cultivation of a wetland, if accompanied by lack of flooded or water-logged conditions that provide the physiological requirements for wetland plant establishment, can thus have the dual effect of germination stimulus and lack of replenishment. Although wetlands retain a seed bank after cultivation, key structural species, specifically tussock-forming species, can be lost (Wang et al. 2013).

Repeated disturbance and stimulus of germination, without replenishment (as might occur in annually cultivated soils) is likely to rapidly reduce the diversity and abundance of wetland seed banks (Waters et al. 2010). Wetlands in farmed or cultivated landscapes generally have lower quantities of seed (Wang et al. 2013), lower diversity and establishment densities (Casanova 2012) than natural or restored wetlands. There is little likelihood of seed survival after 20 years of continuous cultivation (Donath et al. 2003), and significant decline can occur after only a few years (Casanova 2012). Cultivated wetlands, especially those that have been cultivated several times, thus have a very low regeneration potential from the sediment seed bank, and would be reliant on seeds dispersing into the wetland.

Granivory

Propagules in the seed bank are killed mainly by exhaustion of reserves (Bell and Clarke 2004, Leck and Schültz 2005). Fungal infection and possibly invertebrate granivory (seed consumption) could also be important (Leck and Schültz 2005). However, it is difficult to assess granivory in the seed bank, so it is not generally measured except to record viability after storage (Bell and Clarke 2004). Compared with the mortality rate in germinating seedlings, granivory is probably insignificant. It is only likely to be an issue in wetlands that have been dry, of floodplains that have not been much flooded (e.g. Meeson et al 2002) and have built up ant populations, and where direct seeding is being considered.

Grazing

Grazing by animals often results in the loss of reproductive structures, which can reduce the abundance of seeds of species vulnerable to grazing and increase the abundance of species that are resistant to grazing or facilitated by grazing (Nicol et al. 2007). Some plants respond to grazing by increasing their reproductive output, which can result in high densities of seeds of these species in the seed bank. Examples of this are sedges such as *Cyperus difformis* (Eldridge and Lunt 2010) and *C. sanguinolentus* (Warwick and Brock 2003), particularly of semi-arid zone wetlands (Eldridge and Lunt 2010, Waters et al. 2010). On the other hand, many temporary wetlands retain diverse and abundant seed banks despite long-term grazing by domestic stock (Casanova and Brock 2000, Waters et al. 2010, Brock 2011, Casanova 2012, Casanova 2015). The consequences of grazing on seed banks are difficult to predict without considering the duration and intensity of grazing, the species of grazer, local climatic conditions and adaptations of the local flora (Casanova 2006).

4.3.4 Role of water regime on germination from the seed bank

Water regime largely determines, the suite of species that germinate and establish from the seed bank and their abundance (Casanova and Brock 2000, Nicol et al. 2003). The depth to which seed banks are inundated, the duration of water-logging or inundation, the frequency of water level fluctuations, the rate of water level change, the direction of change (wetting or drying) and the season of inundation can all have significant effects on the plant community that emerges (Casanova and Brock 2000, Britton and Brock 1994, Nicol et al. 2003). These factors are responsible for the zonation of species in wetlands with fluctuating water levels (Moore and Keddy 1988, Rea and Ganf 1994, Nicol and Ganf 2000). In general fewer species establish under continuous flooding, and more species establish where soil remains water-logged, or there is variation in the water-level during the establishment phase (Casanova and Brock 2000, Nicol et al. 2003).

4.4 Diversity for restoration success: current concepts

Until recently, the standard advice for sourcing plant propagules was to use local provenances, based on the premise that genotypes that are endemic to the region are more likely to successfully colonise the site (Lesica and Allendorf 1999). However, recent research (Gross et al. 2016) has shown that providing a diversity of genotypes can be a more effective strategy for vegetation recovery because of the diversity of responses and tolerances that plants of the same species from different provenances can provide.

Weeds, or species growing 'out of place' can be a problem in wetland restoration, particularly when a hybrid or novel genotype emerges that is able to effectively invade and compete with native species, as has happened in coastal marshes of North America with *Phragmites*. There are genotypes of *Phalaris, Typha* and *Phragmites* that can be particularly invasive in disturbed wetlands (Lavergne and Molofsky 2007, Saltonstall 2002, Travis et al. 2010).

4.5 Seed bank and restoration

Current vegetation, which includes the seed bank, is essential for vegetation restoration at a site. Although the major constituents of a wetland could be manually planted, or arrive via vectors, (as happens when a wetland is created naturally), restoration is likely to take decades (Section 2.2.2) and relies on the maintenance of natural processes and pathways, and a connected landscape. Successful dispersal depends on connectivity and reestablishment of processes that maintain or restore biodiversity, and this can be hindered by legacy conditions such as water chemistry or weed infestation.

Vegetation types that are likely to be more difficult to restore using seed banks occur in permanent wetlands with stable water levels, such as bogs, springs, heaths and lakes, because their seed banks are believed to have a low density and low diversity. Wetlands that have been impacted for longer (e.g. drained, cropped or permanently flooded) are likely to have depleted seed banks and therefore require more than seed banks for vegetation recovery; and wetlands where the woody vegetation is in poor condition or absent altogether are likely to require addition of seeds or plants from other sources. Where restoration of water regime does not facilitate change in the dominance of particular competitive herbaceous species, active removal of competitive species could allow establishment of more desirable vegetation from the seed bank.

5 Climate change and vegetation recovery

5.1 Background

Climate is a driver of wetland plant communities, and arguably the most influential one. It affects wetland plants in two ways. It influences plant growth, through the regulatory effect of temperature and relative humidity on photosynthesis, growth rate and water relations; and it provides habitat, through rainfall, evapotranspiration, wind and temperature which collectively determine the water balance of a wetland. Wetland plants are thus particularly vulnerable to climate change.

The influence of climate on wetland plant communities varies across Australia, and between landscapes. In upland and montane areas, temperatures are low for much of the year and the growing season is short. Montane shrubby bog wetlands in northern NSW are maintained by specific ranges and combinations of climate variables, mostly to do with temperature (Hunter and Bell 2013). Sphagnum bogs in the ACT and Victoria occur under quite specific temperatures that influence sphagnum growth, constrain shrub invasion and foster organic matter accumulation (Whinam et al. 2003; Macdonald 2008). In inland areas and most lowlands, high rather than low temperatures are an issue. However, one adaptation for ameliorating the stressful effects of high temperatures on leaf function is transpirational cooling, which requires plentiful water. Hence the availability of wet habitats is a major influence on the occurrence and growth of wetland plants in hot areas.

5.1.1 Climate change in Australia

The most recent projections for climate change are downscaled from global climate models to regions across Australia, referred to as clusters (CSIRO and BOM 2015). These projections are reported, with confidence levels, for different future CO_2 trajectories (known as representative concentration pathways or RCPs), with RCP 8.5, RCP 6.0, RCP 4.5 and RCP 2.6 corresponding to CO_2 equivalent concentrations of 1370, 850, 650 and 490 ppm in 2100.

Multiple lines of evidence (IPCC 2014) show that the world's climate has already begun to change. Since 1910, Australia has experienced a rise in average annual temperatures (Figure 9), warmer nights, more extreme temperatures, more hot days per annum (days when the temperature is more than 35 °C), and a fire season that is now longer than it was in 1974 (CSIRO and BOM 2016).



Figure 9: Change in annual mean temperature since 1910 (CSIRO and BOM 2016).

Rainfall for the wet season in northern Australia has been either highest on record or very much above average, whereas southern Australia has been in a drying trend: in south-west Western Australia the late autumn early winter rainfall since 1970 is 19% less than long-term average (CSIRO and BOM 2016). The trend for all parts of Australia is to become warmer and for southern areas to become drier (northern areas being still uncertain in modelling) (Appendix 3).

The extent of warming in the near future is expected to be about 1 °C in annual average temperature in the next 15 years under intermediate CO_2 concentrations (range 0.5 to 1.4 °C by 2030) and could be as much as 2.3 to 5.4 °C by the end of the century, under a high CO_2 concentration scenario. This will be accompanied by a two to three-fold increase in the number of days above 35 °C. In the southern half of the continent there will be a decrease in winter–spring rainfall as winter storms move southwards, as well as more time in drought conditions. Across Australia, potential evapotranspiration is expected to be higher throughout the year. The consequences, especially in southern areas, will be lower humidity and worse bushfire weather.

This warming has already started to affect Australian biota. For example the distribution of the Platypus has changed (Klamt et al. 2011), and CO₂ enrichment has increased vegetative cover in parts of Australia (Donahue et al. 2009).

5.1.2 Effects of climate change on wetland plants and wetland plant communities

Worldwide, knowledge about the effects of climate change on wetlands has increased enormously over the last five years. Much of this is to do with methane fluxes and carbon sequestration in high latitude wetlands such as bogs, fens and peatlands, or with salinisation and marine inundation of coastal wetlands, saltmarshes and mangroves caused by sea level rise. Relatively little work has been done on inland wetlands, and investigations have concentrated on significant wetland systems such as the Florida Everglades or the Northern Prairie Potholes, with a few reviews done for particular types of wetland plant communities: submerged and emergent macrophytes (Short et al. 2015) and wet grasslands (Joyce et al. 2016).

In Australia there have been overviews and syntheses on climate change and its ecological effects, most notably the landmark review by Hughes (2003). There have also been investigations into surface water resources of individual catchments within the Murray–Darling Basin as part of the Sustainable Yields Project, and of groundwater resources (e.g. Barron et al. 2011) and, to a lesser extent, consideration of water quality (Hobday and Lough 2011). Inland wetlands have been included in these, although not in much detail, and they have also been included in critiques of policy, scoping management options and outlines of research needs (Jin et al. 2009; Jenkins et al. 2011; Finlayson et al. 2013). Most of these have drawn on climate projections from the fourth IPCC and predict a rainfall decrease across southern Australia.

The ecological consequences of climate change and of carbon dioxide enrichment on inland wetlands have not received much attention. The likely effects of climate change for regional wetland systems have been synthesised by Finlayson et al. (2013), for inland wetlands in south-eastern Australia by Jin et al. (2009), for riverine and riparian vegetation by James et al. (2016), and for floodplain and wetland fauna of the Lower Murray by Gonzalez et al. (2011). Due to the lack of relevant research, the syntheses have been reliant on applying existing ecological knowledge to hydrological modelling.

Hydrological modelling has been used to predict likely changes in river flows, floodplain inundation and wetland connectivity for parts of south-western Australia, Victoria and northern Australia (Barron et al. 2012; DSE 2013; Karim et al. 2015a,b), and the outputs used to make limited ecological inferences. Decision support tools that have been developed to assist environmental watering for large floodplain wetlands in the Murray–Darling Basin (e.g. Merritt et al. 2010) combine hydrological and inundation modelling with ecological response models (usually limited to ecological condition), and can also be used to explore the effects of climate change on vegetation condition by running a future hydrology time series (Fu et al. 2015).

A different type of modelling, called conceptual modelling, was used effectively at a landscape scale to explore the effects of altered hydrology and altered water quality on persistence and sustainability of wetland vegetation (Nielsen and Brock 2009). There are only a few studies investigating climate change (e.g. Nielsen et al. 2015, Dessent 2016).

Carbon dioxide (CO₂) is also a matter of concern. The widely accepted definition of climate change is 'A change in the state of the climate that can be identified (e.g. by statistical tests) by changes in the mean and/or variability of its properties, and that persists for an extended period of time, typically decades or longer' (CSIRO and BOM 2015). This definition excludes greenhouses gases such as CO₂ that drive the radiative balance of the Earth. The concentrations of CO₂ have been increasing since the middle of the 19th century when they were less than 300 ppm. Globally-averaged concentrations are currently nearly 400 ppm

and are projected to continue to increase for some time to come (IPCC 2014). High concentrations of CO₂, referred to as *carbon dioxide enrichment*, are not included in climate change projections but their impacts need to be considered concurrently with climate change because of its importance for vegetation.

The following sections present the likely effects of CO_2 enrichment and climate change (temperature, rainfall) on wetland plants and communities (effects which are quite intricate) as these relate to wetlands of inland Australia, then draw out the implications for vegetation recovery. Other aspects of climate change such as changes to Ultraviolet band B and bushfire behaviour, although relevant are not covered.

5.2 Carbon dioxide enrichment

5.2.1 CO₂ and plants

Some plant species with leaves in the air have evolved carbon-concentrating mechanisms (CCMs) to overcome photorespiration, which is an energy-wasteful process: the principal CCMs are referred to as C2, C4 and CAM. Plants with no CCM are C3 plants. These CCMs differ in energy efficiency, use of nitrogen, and water use efficiency (Sage and Stata 2014). For plants that have leaves growing in water, carbon is limited by the rate of diffusion in water, which is 10 000 times slower in water than in air (Armstrong 1979). As a result, submerged plants also have mechanisms for increasing CO₂ concentrations within the plant. These involve pumping dissolved inorganic carbon (DIC), which is known as HCO₃ utilisation.

The majority of the world's plant species are C3 plants. C2 plants are quite rare; there are only about 40 species, all herbs of hot environments. C4 plants are more numerous, with about 7500 species of grasses, sedges and herbaceous shrubby species from warm to arid environments, but no trees (Sage and Stata 2014). The majority of C4 plants are monocots such as grasses and sedges. Some C4 grasses such as *Echinochloa crus-galli* and *Paspalum distichum* are serious environmental and agricultural weeds in parts of Australia. CAM plants number about 20 000 species: although most are succulents of very dry environments, a few are aquatic plants including *Crassula helmsii* and *Isoetes australis* (Pedersen et al. 2011). The DIC pumpers are the most numerous among wetland plants, with 72 000 species, but these are a mix of algae and submerged macrophytes (Sage and Stata 2014).

However because carbon concentrating mechanisms also consume energy, C4 plants are more energyefficient than C3 plants only under drier conditions, where they have higher rates of photosynthesis despite increased resistance of stomata. Under wet conditions, where stomatal opening does not present a risk to the water balance of the plant, the advantages of CCM are diminished. Competitive interactions between C3 and C4 plants will be altered by CO₂ enrichment, and it is anticipated that CO₂ enrichment will favour C3 plants more than C4 plants (Arp et al. 1993).

Carbon dioxide concentrations are not growth-limiting for plants with leaves in the air but can be for plants that grow wholly submerged, such as some macrophytes, ferns, lichens and bryophytes. Submerged macrophytes have the capacity and flexibility to use more than one CCM at a time, even within one leaf, as in *Vallisneria americana* (now *V. australis*), depending on whether the leaf is in bright light at the water surface or not (Barrett 2007).

Submerged macrophytes that use only CO_2 are obligate CO_2 users, whereas those that use CO_2 and HCO_3 are facultative HCO_3 users (Schippers et al. 2004). The capacity to utilise HCO_3 makes it possible to photosynthesise across a wider pH range than obligate CO_2 users. Submerged macrophytes known to be HCO_3 facultative in Australia include native species such as *Vallisneria australis* and *Potamogeton tricarinatus* (Barrett 2007) as well as significant environmental weeds such as *Egeria densa* and *Elodea canadensis*.

5.2.2 Effects of CO₂ enrichment

Carbon dioxide enrichment is expected to stimulate photosynthesis, though just how much depends on the species and what photosynthetic pathway it has (Sage and Kubien 2003). If it is a submerged macrophyte, then the effect depends on whether it is an obligate CO_2 species or facultative HCO_3 user (Schippers et al. 2004) or one of the few species (such as isoetids) that can obtain its CO_2 from the sediment (Short et al. 2016). The size of the response will also be influenced by environmental context, such as whether the site is eutrophic, how much atmospheric CO_2 enrichment is transferred to the waterbody (Schippers et al. 2004), and on regional climate (Drake 1992). These expectations and projections are given in more detail below (Table 3).

Table 3: Variable effects expected of CO₂ enrichment on plants.

Type of plants	Expected effects
Terrestrial plants (foliage in air) (Sage and Kubien 2003)	Direct stimulation of photosynthesis (C3 more than C4). Direct stimulation of growth (C3 more than C4). Reduction in stomatal conductance (C3 and C4 similar).
Submerged plants (foliage underwater) (Schippers et al. 2004)	CO_2 obligates benefit more than HCO_3 facultative, and HCO_3 facultative plants benefit more than algae.
Plants in small eutrophic systems Oligotrophic softwater systems, with isoetids Short et al. (2016)	Increased growth in floating plants, and shading out submerged macrophytes. Shift in species composition, due to isoetids being replaced by species (such as milfoils) that are more effective at uptake of carbon dioxide. Isoetids typically take up CO ₂ from sediment.

Carbon dioxide enrichment is known to be affecting the chemistry of the ocean, with pH expected to fall by 0.2-0.3 units by 2100 (Hobday and Lough 2011), but its effect on inland waters is not much considered. According to Schippers et al. (2004) the effect will be variable. Waterbodies likely to have higher CO₂ concentrations are those that are turbulent rather than standing (i.e. lotic versus lentic) such as upland streams and down-wind lake shores, waterbodies that are not so dependent on air CO₂ for their carbon supply, such as waters with high alkalinity and community respiration, and waterbodies where other nutrients are not limiting, such as systems that are productive and nutrient-rich.

The contrasts of particular interest in anticipating the effects of CO₂ enrichment are:

- CO₂ obligates versus HCO₃ facultative submerged aquatic plants (Schippers et al. 2004)
- C3 versus C4 terrestrial plants (Sage and Kubien 2003)
- native versus exotic species (e.g. Blumenthal et al. 2013).

Stimulation of photosynthesis can have significant ecological consequences, not just for individual species but in how they interact and how ecosystems function. Increased growth under CO_2 enrichment and higher temperatures is likely to result in:

- higher biomass and greater productivity; changes in plant tissue composition, specifically higher C : N
 ratios, which might have consequences for dependent herbivores, decomposition rates and litter
 accumulation
- altered species interactions which could lead to shifts in community dominance, changes in floristic composition, and boundary shifts between C4 grasslands and C3 forests and woodlands
- interactions between native and introduced or invasive species becoming more extreme
- salt stress alleviation in some C3 species.

5.2.3 Current knowledge

Studies of CO₂ enrichment on wetland plants and wetland systems are presented below (Table 4), including whether the study species is C3 or C4, as reported in the original paper. No Australian studies are included as none were located dealing with wetland plants. The findings broadly match expectations. Carbon dioxide enrichment on its own has a relatively small effect on growth, but the effect is much greater when coupled with higher temperature. Tissues of CO₂-enriched plants have higher C : N ratios than unenriched plants in C3 species but not in C4 species (Drake 1992, Drake 2014). Shifts in dominance, away from *Sphagnum* and towards *Carex* and graminoids occurred in a fen peatland (Eriksson et al. 2013).

The longer time-frames of field experiments give a better understanding of temporal aspects such as seasonal effects and phenology than can be achieved by short-term physiological studies. Many field experiments follow the international protocol for outdoor CO₂ enrichment, known as FACE (free air CO₂ enrichment), such as for sphagnum (Berendse et al. 2001). Outstanding in this regard is a field experiment on CO₂ enrichment on brackish coastal marsh vegetation in Chesapeake Bay that has been running for 28 years and has documented not just vegetation effects but ecosystem adjustments (e.g. Drake 2014).

Table 4: Studies on CO₂ enrichment and wetland plants.

Purpose	Study details	Response to CO ₂			
Effect of elevated CO ₂ (550–600 ppm) on invasiveness under low nutrient conditions typical of coastal wetlands. Sullivan et al. (2010)	Comparison of 3 <i>Typha</i> taxa: native versus introduced versus hybrid <i>Typha</i> spp One year; using open top chambers, on a hill top	No evidence of any taxa being more affected by CO ₂ elevation. Rhizome biomass increased by 40% for all taxa in the following year. No effect of CO ₂ on above-ground production: plants possibly nutrient- limited.			
Effect of elevated CO ₂ (ambient + 330 ppm) and nitrogen eutrophication. Comparison of native and introduced genotypes. Mozder and Megonigal (2012)	Hypothesised that the introduced genotype would respond more positively to elevated CO ₂ , and N (separately, then together) than the native genotype <i>Phragmites australis</i> Emergent macrophyte C3 plant Over midsummer (June to August), in a greenhouse	 Both genotypes responded positively to CO₂, to N addition, and to CO₂ + N. Introduced genotype grew more, and outperformed native genotype for 13 out of 15 traits, across all resource availability tested. C:N ratio was highest (>20:1) in elevated CO₂ treatment, falling in nitrogen treatments to about 16 : 1. Inferred that the introduced genotype is more plastic than native genotype. 			
Effect of elevated CO ₂ (700 ppm) and temperature (+5 °C) on native and invasive clones; with salinity as stressor Eller et al. (2013)	<i>Phragmites australis</i> Emergent macrophyte 151 days, in phytotron	Elevated CO ₂ had almost no effect on aboveground material of any clone. Combination of elevated CO ₂ and higher temperature stimulated growth and aboveground biomass in both clones. Native clone shows greater plasticity.			
Effect of elevated CO ₂ (681 ppm) on ecosystem processes (carbon budget, competition) on three communities in one saltmarsh Drake (1992)	Scirpus olneyi and Spartina patens Emergent macrophyte and saltmarsh grass A C3 sedge, a C4 grass Field for 4 years, with open- top chambers	Elevated CO ₂ increased photosynthetic capacity, decreased respiration, reduced N-content and altered nitrogen economy of C3 sedge but not C4 grass. Elevated CO ₂ resulted in higher aboveground and root biomass, and larger annual carbon budget in C3 sedge. No effect on C4 grass.			
Testing for CO ₂ limitation, even in HCO ₃ using plants. Hussner et al. (2016)	Ten species Submerged macrophytes (all HCO ₃ users) Laboratory, for 35 days	Growth rate stimulated under both CO ₂ treatments. All plants allocated more biomass to roots, under additional CO ₂ . Tissue nitrogen concentration was lower under higher CO ₂ availability.			
Effect of CO ₂ and N enrichment on sphagnum, and on carbon sequestration Berendse et al. (2001)	Sphagnum and co-occurring species Field sites across Europe	No effect of CO ₂ enrichment on sphagnum biomass or growth. N enrichment stimulated other bog plants more than sphagnum. Sphagnum growth inhibited under N- enrichment due to competition.			

5.3 Warming

5.3.1 Temperature and plants

Temperature determines the rate of metabolic processes such as photosynthesis and respiration, and thus affects every stage in the plant life-cycle. Species have individual responses to temperature in terms of the range tolerated, critical thresholds, and the optimal temperature for photosynthesis and growth. Plants photosynthesise over a broad temperature range, such as below 0 to 30 °C for cold-adapted plants, and 7 to 40 °C for plants from more temperate areas, but within these ranges they have a thermal optimum which can shift through acclimation (Sage and Kubien 2007). Minor differences in optimal temperatures between co-occurring species can determine the outcome of species interactions such as competition.

Temperature may also act as an ecological cue that initiates a phenological stage or triggers a life history stage, such as germination, the formation of perennating organs such as turions, or flowering. Often the trigger is a combination of a critical threshold temperature or accumulated warmth (such as growth degree days) with another environmental signal such as photoperiod, light intensity or light quality.

Seed germination and seedling establishment are particularly vulnerable stages in the plant life cycle, and seed dormancy is a mechanism to minimise the likelihood of germination at an unfavourable time. Of the five classes of primary dormancy recognised by Baskin and Baskin (2004), the most common in wetland plants is physiological dormancy, which requires stratification combined with other dormancy-breaking factors (Merritt et al. 2014). However not all seeds are dormant: *non-dormant* seeds are those that do not have any specific requirements but germinate readily in the presence of appropriate light, temperature and moisture. Groups of similar germination traits form a germination syndrome, and different syndromes may occur in the same wetland (e.g. Ferandez-Pascual 2016).

Examples illustrating the role of temperature at different stages in the life-cycle of wetland plants are shown below (Table 5), using Australian examples where possible. Australian studies have concentrated on the early stages, on seed banks and germination; most studies on the effects of temperature on photosynthesis, growth and production date from the 1980s.

Life-cycle stage	Study details	Role of temperature
Seed bank viability Salter et al. (2010)	Submerged macrophyte <i>Vallisneria australis</i> Gippsland Lakes, Victoria	Germination from seedbank greatly reduced if exposed to high temperatures (35 °C) during the wetland dry phase as this reduces the germination rate from 44% to 7%. Temperature effects on seed viability in sediment thus defines the timing of successful drawdown.
Germination Britton and Brock (1994)	Species assemblage Upland lagoons, NSW Outdoor experiment	Species richness and abundance of seedlings emerging from sediment seedbanks was lowest in summer, highest in autumn. Low values for summer interpreted as an adaptation against exposing seedlings to midsummer heat and water stress in the event of a drawdown.
Germination Vincent (2012)	Floodplain trees Murray-Darling Basin Laboratory experiment	Germination is higher under fluctuating temperatures than constant. Species have differing thermal regeneration niches: Optimal diurnal (day-night) range for <i>E. coolabah</i> is 30–15 °C, and for <i>E. largiflorens</i> is 35–20 °C.
Germination Tuckett et al. (2010)	Nine macrophytes Temporary pools, WA Laboratory experiment	Two germination strategies present: <i>non-dormant</i> , and <i>dormant</i> . Non-dormant species germinated over all temperatures tested (5 to 20 °C) but differed in which was optimal. Germination strategy and dormancy requirements were not aligned to phylogeny: genera <i>Glossostigma</i> and <i>Myriophyllum</i> had dormant and non-dormant species. Dormant species germinated after warm stratification but not cold stratification.
Seedling Success Ter Heerdt et al. (2017)	Emergent macrophytes (<i>Typha, Phragmites</i>) and mudflat herbs Climate chambers, The Netherlands	Temperature conditions during early establishment determine final assemblage, due to species differences in growth rates, emergence and temp responses. Cool wet or moist conditions favour emergent macrophytes: but if warmer then mudflat herbs also establish, resulting in more diversity.
Growth Orr et al. (1988)	Submerged macrophyte <i>Myriophyllum</i> salsugineum Glasshouse experiment, Griffith, Australia	Light compensation point, which is the irradiance level at which photosynthesis balances respiration, increases exponentially with temperature. Optimum temperature for growth is around 30 °C.
Competition Riis et al.	Submerged macrophytes Invasive species (3) in	Summer temperature a strong effect on rate of photosynthesis. Summer temperature not as strong an effect on growth as

Table 5: Examples of the role of temperature on wetland plant life-cycle.

Life-cycle stage	Study details	Role of temperature
(2012)	family Hydrocharitaceae	light. Species difference in response to light and temperature used to make inferences about type of seasonal conditions where each would have a competitive advantage.
Competition Breeuwer et al. (2008)	Sphagnum (four species) Europe Greenhouse experiment	Increasing temperature resulted in more biomass and greater height in all four species. Competitive balance between three of the four species affected by temperature.
Distribution Riis et al. (2012)	Submerged macrophytes Invasive species (3) in family Hydrocharitaceae	Distribution of invasive aquatic plant <i>Lagarosiphon</i> in New Zealand probably controlled by summer temperature.
Persistence Chambers et al. (1985)	Submerged macrophyte Laboratory experiment Scotland	Turion formation in <i>Potamogeton crispus</i> is under dual control of photoperiod and temperature. No turions formed if daylength is <12 h, or under 16 °C.

5.3.2 Effects of warming

The consequences of warming depend partly on location and partly on the temperature responses and capacity for acclimation of individual species. Higher temperatures will generally result in faster photosynthesis and more growth, especially for plants in cool temperate areas and uplands. In these areas the constraining effects of low temperatures, frost days, snow cover and a short growing period will be relaxed, creating an opportunity for general upwards (altitudinal) colonisation as well as locally downward into frost hollows.

In areas that are already warm or hot, warming could result in optimal temperatures for growth being exceeded, so would not necessarily result in increased growth. The very individualistic response of species to temperature has been shown for two closely related and sympatric submerged macrophytes: *Ceratophyllum demersum* was able to acclimatise by raising its thermal optimum, whereas *C. submersum* was unable to sustain such an adjustment (Hyldgaard et al. 2014).

Life history stages such as germination will be affected. Dormant species that require warm stratification to germinate, such as *Glossostigma trichoides* (Tuckett et al. 2010), and non-dormant species with a higher optimal range, such as *Eucalyptus largiflorens* (Vincent 2012) will be advantaged over those requiring cold stratification or have a lower optimal temperature.

Lethal effects and periods of stress will be increased, as what was once a brief or rare occurrence of unusually high temperature will become more frequent or extended. Extreme heat can have lethal effects on sediment seedbanks by causing seed deterioration through protein denaturation (Visscher et al. 2016). Seeds generally do not survive exposure, even if only brief, at temperatures of 150 °C which commonly occurs in a bushfire. At a depth of 40 mm, temperatures can peak at just over 80 °C and stay above 60 °C for an hour (Newton et al. 2006).

5.3.3 Current knowledge

The importance of temperature for plants is understood in general terms, but species-specific thresholds or optima are virtually unknown and inadequate to scope the effect of climate change on wetland vegetation, except in broad terms.

The very large numbers of studies on seeds germinating from seed banks in eastern and southern Australia without using a stratification treatment suggests that the majority of wetland species (at least in southeastern Australia) are not dormant. However, an investigation into temperature effects on nine species from temporary wetlands in Western Australia found that only five were not dormant, and that the other four had specific dormancy-breaking requirements including warm or cold stratification (Tuckett et al. 2010).

Flowering time in *Eucalyptus* trees from wet and dry sclerophyll woodlands is determined by climate, specifically by the mean temperature in the preceding three months (Rawal et al. 2015). A one degree rise in temperature can shift flowering time by as much as 14 days, with some species flowering earlier and some later. The likely outcome of warming on these sclerophyll woodlands is thus a re-arrangement of when nectar and seeds will be available for dependent fauna such as birds and insects. Riparian woodlands are

also important as a floral resource for birds, but it is not known whether temperature is a flowering cue for floodplain and riparian species.

In relation to seedbank viability, two studies have recently established that wetland sediment seed banks from south-eastern Australia have a temperature threshold of 70 to 80 °C, above which germination fails (Nielsen et al. 2015, Dessent 2016). This threshold is considerably lower than the critical temperatures suggested from accelerated ageing techniques (Visscher et al. 2016), and suggests that sediment seed banks might not be a reliable determinant of resilience and recovery, especially in a warming climate.

5.4 Altered rainfall

5.4.1 Rainfall and plant habitat

Rainfall is the source of water for inland wetlands, and it reaches a wetland by one of three pathways: by falling directly, by overground flow, or by moving through the ground. These pathways are equivalent to the three types of water sources used in the Australian National Aquatic Ecosystem (ANAE) classification framework: localised rainfall, surface water, and groundwater (Aquatic Ecosystems Task Group 2012).

These pathways have distinctive spatial and temporal characteristics that influence how quickly a wetland responds to rainfall, and how its water quality might be affected. Wetlands with little to no catchment ('localised rainfall' in ANAE) respond quickly to rain, their water levels rising within hours to days. Wetlands fed by run-off or river flows have a lagged response, their water levels rising days, weeks or even months after rain. Billabongs that fill by floods in arid-zone rivers may be responding to rainfall several hundred kilometres away, and montane and upland streams that flood with spring snow-melt are responding to snowfall that happened months earlier.

Wetlands fed by groundwater also have a lagged response, ranging from days to weeks if fed by local groundwater such as for seeps and recharge springs, to months and years if fed by regional groundwater (DSE 2013). An extreme example of temporal lag comes from the Great Artesian Basin, where it takes 1 to 2 million years for rain falling in the Queensland recharge area to discharge in mound springs in South Australia, several hundred kilometres away (Fensham and Fairfax 2003).

The hydrological, hydraulic and water quality characteristics of a wetland determine what plants grow there, hence water regime is considered an environmental filter (e.g. Nicol et al. 2003; Raulings et al. 2010). Duration of inundation defines the length of time available for growing to reproductive maturity and producing propagules or recharging a rhizome: duration of the dry phase determines whether a species can regrow from rootstock, tuber or corm, whether its propagules are still viable in the seedbank. Hydrological connection to other wetlands allows dispersal of propagules such as seeds and vegetative fragments and allows genetic mixing (Morris 2012); however, although hydrological connectivity is perceived as being ecologically important, it does not appear to be important in structuring vegetation composition in northern Australian wetlands (Reid et al. 2016, Warfe et al. 2013). Hydraulic characteristics such as depth strongly influence where in a wetland a species can grow. Rhizomatous emergent macrophytes, with leaves in air and roots in sediment, can grow in water up to 3 m deep if they are capable of pressurised ventilation, but are restricted to depths of less than 1 m if not (Brix et al. 1992, Sorrell and Hawes 2010). Differences between species in their depth preferences determine the outcome of competition between native species as well as between native and exotic species (e.g. Price et al. 2011). Adaptations such as flexible stems, resource allocation, constant leaf recruitment and sacrifice (e.g. Cooling et al. 2001) allow species to grow where water levels fluctuate. Water quality characteristics such as clarity and nutrient status determine growing conditions, especially for submerged plants (e.g. Morris et al. 2004).

Wetland plants have an enormous range of physiological and morphological adaptations and ecological strategies for growing in a wetland, and this is part of the diversity of wetland plants. Descriptions of these adaptations and strategies can be found in Capon et al. (2016) and Cronk and Fennessy (2001). The Australian studies listed in Table 6 are a selection to illustrate this diversity. The functional group approach to classifying wetland plants (Casanova and Brock 2000, Casanova 2011) is based on these adaptations and strategies.

Growth, life- cycle and resilience	Wetland habitat and water regime study details	Role of wetland habitat
Resilience: Sediment seed bank viability	Duration of dry phase Upland wetlands 'lagoons' in New England, NSW	Seed longevity for dry-stored seeds ranged from 2 to 13 years (the max tested). Mean was 7.4 years: over 70% of species survived 5 years plus.
Brock (2011)		sharply after 5 years. No relationship between longevity and functional type, or
		longevity and taxonomy. Longevity was similar, whether dry stored or exposed to periodic wetting.
Life-cycle: Establishment	Depth, duration, frequency of inundation.	Experimental range was 5 to 60 cm depth, frequency 0 to 4 times, duration from 0 to 16 weeks.
Casanova and	upland wetlands, New	composition of wetland seed bank.
Brock (2000)	England, NSW	Increasing depth, and/or increasing duration and/or increasing frequency act to progressively exclude terrestrial functional types in favour of submerged functional types
Life-cycle: Establishment	Depth and drawdown rate Seed material from Bool	Experimental range was 0 to 80 cm depth, and drawdown rate was none to slow to fast, over 14 weeks.
from seedbank Nicol et al. (2003)	Lagoon complex, SA	Increasing depth and drawdown rate excluded terrestrial functional types, but favoured submerged and amphibious functional types
Life-cycle: Reaching maturity from seedbank	Depth, duration, timing (season) of inundation Upland wetlands, New England NSW	Season has a significant effect on number of species establishing and number reproducing within time-frame tested (16 weeks): 9 and 2 in autumn compared with 29 and 27 in summer.
Warwick and Brock (2003)	-	Season significant in determining above-ground biomass, which was 5+ more in summer than autumn.
Growth: Seedlings Greet (2015)	Flooding depth and duration Floodplain tree (<i>Eucalyptus camphora</i>) Glasshouse experiment	Seedlings (3 months, 8 months) survived and grew in water- logged and shallow (10 cm) flooding for up to 12 months. Seedlings (1 month) unable to survive being submerged. Growth (height, biomass) optimal in moist soils.
Growth: Seedlings	Flooding depths (0, 5cm and 15 cm, and drying)	Seedlings 3 months old survived and grew in moist and flooding for up to 6 months.
Capon et al. (2009)	and duration Floodplain shrub	Seedlings grew poorly (shorter, less biomass) in flooded treatments, but actual depth (5 cm vs 15 cm) not important.
(2000)	(Mueĥlenbeckia florulenta)	Seedlings in drying treatment had similar heights as in water-logged treatment.
Resilience Blanch (1999)	Water depth Medium tall sedge (<i>Bolboschoenus medianus</i>)	Allocation to perennating organs (tubers and rhizomes) greatest in moist, water-logged and shallow water, and decreased with increasing depth (to 60 cm).
Life-cycle:	Inundation timing (spring	Contrast between native and exotic plant species.
Greet et al.	Riparian assemblages	response to summer flooding than to spring flooding.
(2013)		Number of native species flowering not affected by flood timing, showing degree of plasticity.
		Some native short-lived herbs flowered only after spring flooding (spring-obligates).
Life-cycle	Flood timing and plant life-cycle	Reproductive phenology cued to floods in contrasting climate (tropical, temperate).
Pettit and Froend (2001)	Riparian species	Floods act as secondary dispersal, moving seed to safe site.

Table 6: How habitat affects growth, life-cycle, and resilience: Australian examples.

5.4.2 Effects of altered rainfall

Climate projections for the southern part of Australia (see Appendix 3) are for a shift in the annual rainfall pattern (seasonal effects, intensity increases). When combined with warmer temperatures and increased evapotranspiration, this is expected to result in generally drier conditions. The non-linear relationship between rainfall and run-off indicates that surface-fed freshwater wetlands could be affected more than other wetlands. In south-eastern Australia the expected median change in runoff for 2090 under RCP8.5 is a decrease of about 20% for the southern areas and slightly more for the Murray Basin. However, such estimates have a very large uncertainty range (Timbal et al. 2016).

Changes to wetland plant habitat are likely to be as follows. For wetlands fed by local rainfall, surface water or local groundwater, the water regime is likely to lose its seasonal pattern and become less predictable and more variable. Smaller peak flows down rivers will result in floodplains and riverine wetlands being flooded less frequently, not as deeply, and with much longer dry intervals; some wetlands may cease to be flooded by rivers at all. Soaks, springs and recharge springs sustained by local groundwater will become less wet, flow less often, and contract in area: some may cease to exist. Hydrological connectivity, whether between river and floodplain or between normally isolated wetlands, will be shorter and less frequent: some may cease altogether. At a regional or landscape scale the types of water regimes present will change, with permanent wetlands transitioning to intermittent, and intermittent to episodic; surface-water wetlands with permanent water regimes will be rare or even locally extinct.

The Australian studies summarised below (Table 7) emphasise that these effects will not be uniform, and that the magnitude of the effect will be spatially variable. In Victoria the rainfall-fed wetlands most at risk are in the north-west and south-west of the state (DSE 2013); in Western Australia's coastal regions, groundwater-dependent vegetation most at risk is in the northern-most and southern-most coastal catchments (Barron et al. 2012); and on floodplains, the wetlands with the longest flowpath connecting to the main river channel will experience the greatest reduction in hydrological connectivity (Karim et al. 2015a).

As well as these hydrologic effects there will be changes in water quality: warmer water due to a combination of shallower water and warmer air temperatures; increased turbidity or loss of clarity due to inorganic particulates being washed in following bushfires or due to erosion during intense rainfall; nutrient loading could increase, also as a result of run-off; and salinisation of freshwater wetlands because of increased evapoconcentration combined with less frequent hydrological flushing (Nielsen and Brock 2009). Permanent wetlands with acid sulfate soils will be at risk of acidification and anoxia if they dry out and are subsequently re-flooded (Hobday and Lough 2011). As with hydrologic characteristics, water quality changes such as turbidity and salinisation will be regionalised because they depend on soil characteristics, whereas changes such as warming will be widespread.

Source Metrics	Study details	Modelled effect under given climate change scenario
Volumes of water available to the environment Colloff et al. (2016)	Murray–Darling Basin Scenario is +1.6 °C by 2030	Water volumes will be insufficient to meet most flow thresholds for Basin Plan targets. Magnitude of change ranges from low to very high Southern MDB floodplain wetlands to be more severely affected than northern wetlands.
Hydrological connectivity of floodplain wetlands to river Karim et al. (2015a)	Semi-arid northern Australia Fitzroy River & floodplain	Peak stage height decreased by 0.3 to 0.8 m at downstream gauge. Max area inundated decreased by 4 to 27%, depending on flood. Duration of hydrological connectivity reduced by approx. 20%.
Hydrological connectivity of floodplain wetland to river Karim et al. (2015b)	Semi-arid tropical climate, northern Australia Flinders and Gilbert Rivers & floodplains	 Adjacent catchments show similar types of changes but differ in magnitude. Maximum streamflow reduced by 13% (Gilbert) and 37% (Flinders). Average depth of inundation decreased by 0.6 to 7.2% (Gilbert) and by 2.5% (Flinders) and varied between floods. Average extent of inundation decreased by 9.9 to

Table 7: Effects of a drier climate on wetland plant habitat: Australian examples.

Source Metrics	Study details	Modelled effect under given climate change scenario
		20.9% (Gilbert) and 14.7 to 38% (Flinders), dependent on floods.
		Connectivity decreased by 2.2 to 12.7 % (Gilbert) and 3.9 to 17.7% (Flinders).
Run-off and consequences for dependent ecological systems Barron et al. (2012)	Coastal catchments (Albany to Geraldton) in WA Three climate change scenarios, based on temperature increases by 2030	Periods of no-flow become longer: maximum is an increase of 4+ months in one catchment. Depending on scenario: Area of wetlands under high or severe risk increases from < 5% to 15%: area of groundwater-dependent vegetation at high or severe risk increases by < 5% to 19%.
Inundation and filling frequency (surface-fed, rainfall-fed wetlands). Groundwater-fed wetlands DSE (2013)	State of Victoria, partitioned into five climate regions Dry scenario based on average changes in streamflow 1997–2007, and rainfall reductions from Jones & Durack (2005)	Effect on rainfall-fed wetlands likely to intensify, being more severe by 2050 than by 2030. Filling of rainfall-fed wetlands reduce, variability will increase and dry interval likely to almost double in northwest and southwest regions. Landscape change likely as wetland water regime transitions from a wetter to a drier one. At state-level, impact greatest on rainfall-fed wetlands, least on groundwater-fed wetlands: and on western and northern regions.
Surface water and water quality (salinisation) Nielsen and Brock (2009)	Southern Australia Landscape-scale perspective Warming, and drying but no specific scenario Knowledge-based projection	Some losses, due to some wetlands becoming terrestrial. Shift in mosaic of wetland types at landscape scale: some freshwater wetlands become saline, a few saline may be freshened by falling groundwater levels; a general shift to drier water regimes. Wetlands changing from fresh to saline will have lower plant species diversity.
Groundwater Barron et al. (2011)	Australia-wide aquifers important for utilisation	Inter-annual rainfall variability is magnified 2–4 times in aquifer re-charge variability. Decreases in diffuse recharge likely for southern Australia, increases likely in northern and localised eastern areas. Fourteen aquifers of national importance as a water resource were identified as likely to be highly impacted.
Risks to groundwater- dependent vegetation Barron et al. (2014)	Swan Coastal plain, WA Three climate change scenarios, based on temperature increases by 2030.	 Vulnerability depends on groundwater depth, with greatest risks associated with deeper watertables. Under the driest climate change scenario tested, the area of groundwater dependent terrestrial vegetation under severe to high risk is expected to increase to 10%, 21% and 38% for watertables currently 0–3 m, 3–6 m and 6–10 m deep.

These hydrological and hydraulic changes will, in time, force changes in wetland plant communities. Shorter durations will lead to reduced vigour and cause a shift to species with shorter life-cycles, or that tolerate shorter inundations, or that take a short time to become reproductive. Longer and more variable dry phases will favour species with longer-lived propagules, and provide opportunities for terrestrial species to establish, even temporarily. Hydrological isolation and fragmentation will exclude species dependent on hydrological connectivity for dispersal and favour species dispersing by wind or animal vectors; on floodplains, communities will shift from flood-dependent to flood-tolerant. Similarly, water quality changes will also impose changes through time: turbid conditions will lead to a shift away from species that grow underwater (benthic plants, submerged macrophytes); salinisation will exclude freshwater species, which will be eventually replaced by halophytes. These changes will apply to native and introduced species.

5.4.3 Current knowledge

Largely in response to river regulation, supporting environmental flows, and the recent 'millenium' drought, an extensive body of knowledge has been built up over the last 15 years about the relationships between water regime (surface and groundwater) and wetland and floodplain plants and communities. This body of knowledge is somewhat biased, towards particular species and locations, a situation that has not changed much in fifteen years when compared with an earlier evaluation (Roberts 2001). For example, a large proportion of this has focused on species-level knowledge such as tolerances and life-history, rather than on populations or communities and the processes maintaining them. Knowledge of River Red Gum *Eucalyptus camaldulensis* var. *camaldulensis*, a keystone tree on the floodplains of the Murray–Darling Basin, has increased massively, but this is not true for most other wetland and floodplain species, especially submerged macrophytes. Emerging themes are plasticity, resistance, and processes of invasion. The abundance of introduced species correlates with reduction in flood magnitude (Catford et al. 2014) but cannot be readily linked to functional traits. Most of this knowledge is about floodplain and wetland plants in surface-fed wetlands in the Murray–Darling Basin and south-eastern Australia, as well as groundwater-fed communities of the peri-urban coastal plains of Western Australia.

5.5 Implications for vegetation recovery

The future for wetland vegetation depends on the combined effects of CO_2 enrichment, warming and altered rainfall, and on considering effects at the dual scale of individual wetlands and wetlands within the landscape (Nielsen and Brock 2009). It is fairly clear what the directions of change will be for wetland plant habitats, at least at the local scale; and it is also clear that the biotic interactions and adjustments will be complex, and play out at both wetland and landscape-scale. What is not clear is the rate of change, and what opportunities there will be to manage the transition.

Projections as to what communities will develop where and by when are not feasible without informed modelling, but two predictions can be made. One is that the nature and floristics of wetland plant communities will change. There will be shifts in dominance, individual species will be gradually eliminated from a site, and other species (both native and introduced) will arrive and become established. As with riparian ecosystems (Catford et al. 2013), the outcome will be novel assemblages, floristically different from previous assemblages and probably a mix of native and introduced species, with a functional value that might not be identical to the current mix. Predictions about vegetation recovery are based on current knowledge and make assumptions about each site and its context, such as water regime, and the movement pathways and landscape context (Figure 5).

The other is that the combination of CO₂ enrichment, temperature increases and altered rainfall mean that the wetland as a habitat will change. In Bangladesh, for example, environmental modelling using the MAXENT package found that the freshwater swamp forests of north-east Bangladesh are likely to undergo severe stress and may even become extinct by 2070: the environmental conditions associated with their current distribution are projected to no longer exist for one species by 2050, and to be chronically reduced for the other species (Deb et al. 2016). In the Florida Everglades, hydrological modelling shows that future water levels may be as much as 1.2 m lower or 0.3 m higher, depending on whether a dry or a wet climate scenario is used: however, as the wetland system is believed to be sensitive to inter-annual water level variability, hydrological changes that shift this by 0.25–0.3 m or more may be enough to precipitate extensive vegetation change (van der Valk et al. 2015).

Large changes in wetland vegetation will have consequences for dependent fauna such as waterbirds and amphibians. The Prairie Pothole region of North America is a wetland landscape that is a highly significant waterfowl breeding area, and has been described as 'the single most productive habitat for waterfowl in the world' (Johnson et al. 2005). Climate-sensitive models linking vegetation dynamics to wetland hydrology show that suitable breeding conditions are likely to undergo a major geographic shift, from what has been a breeding stronghold to areas where breeding opportunities will be constrained because wetlands will be largely drained (Johnson et al. 2005).

Because of its role as a driver of wetland functioning, changes to wetland vegetation will also affect ecosystem functioning. Simulation modelling of ecosystem functioning is challenging, and instead projections based on past research and informed by research, opinions have been used. Two examples, for Arctic wetlands (Wrona et al. 2006) and lakes in the Netherlands (Mooji et al. 2005), have been restructured in Table 8 to emphasise the value of separating primary effects from dependencies.

The potential magnitude of climate change and the implications for wetland restoration have been matters of concern for some time. Initially these concerns were to do with the need to protect and maintain existing wetland ecosystems (e.g. Erwin 2009) whereas currently the emphasis is on adaptation. Protection is an

ideal that will require major investment and perpetual vigilance, and hence is an option only for selected sites. Adaptation as an option may be overstated. The adaptive capacity of Australian vegetation is thought to be high, but adaptation might not be feasible because of the expected rate of climate change, compounded by other anthropogenic stressors (James et al. 2016).

Table 8:	Expected	outcomes	of	climate	change	on	wetland	ecosystems.
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Lakes in Netherlands (temperate) Mooji et al. (2005)	Lakes at high latitudes (arctic) Wrona et al. (2006)
Primary producers and their habitat	
Favour cyanobacteria. Lead to botulism, and mosquito-borne diseases. Result in a turbid phytoplankton dominated system. De-stabilise macrophyte-dominated lakes. Mimic eutrophication by an increase in the carrying capacity of primary producers, especially phytoplankton.	Primary production altered due to northern migration of emergent macrophytes. Nutrient and carbon enrichment (especially from permafrost thawing). Status as carbon sink/source likely to change.
Dependent fauna and processes	
Reduce waterbird species richness. Modify higher trophic levels. Adversely affect biota and biodiversity linked to clear water. Suit invading species from a particular region.	Altered habitat quality, affecting aquatic mammals and waterfowl. Altered migration routes. Habitat availability altered. Muskrat abundance expected to increase.

6 Concluding remarks

This review is the first formal attempt in two decades to examine wetland restoration in Australia, since Streever (1997), and it fills a gap. The rationale for undertaking this literature review was to provide a knowledge summary about recovery and wetland vegetation that would then serve as a platform for developing additional tools, such as those described in Section 2. Key principles for wetland vegetation recovery projects and a decision support tool are two such tools arising from this literature review – described below.

Principles for wetland vegetation recovery projects

Four overarching principles are proposed for wetland vegetation recovery projects in Australia, based on this review and those developed by others (Appendix 2). Within each of these guiding principles sits a further set of more specific principles. The guiding principles are relevant to all wetland recovery projects.

Principle 1: A recovery project should have clearly stated ecological goals, with objectives that are SMART (specific, measurable, achievable, realistic and timely).

The paradigm that objectives should be SMART, usually understood to mean specific, measureable, achievable, realistic and timely, applies also to the objectives in a vegetation recovery project.

Set specific objectives

A major finding of this review is the importance of clearly stating the vegetation objective, at the beginning of the recovery project. Without an objective, it is not possible to know if vegetation recovery is on track or whether interventions are necessary; and without a specified endpoint, it is not possible to determine if a project is an ecological success or a failure. Wetland restoration in Australia has had a history of not articulating ecological objectives, and of reporting success as effort expended or as contractual compliance. Such a focus does little to improve restoration practice and provides no evidence that management has arrested the decline in wetland condition evident around Australia (Figure 1).

A parsimonious approach is desirable: one well-thought through and well-articulated objective is easier to work with than an array of poorly expressed objectives. With an array, there is the risk some may turn out to be mutually incompatible.

Objectives that are generalised (such as *establish functionally important species*) or that describe direction or trend (such as *improve vegetation condition* or *increase seed bank diversity*) are indeed an expression of the restoration issue (that functionally important species are missing, that vegetation condition is poor, that the seed bank is depauperate). Although valid as generalised objectives, they need to be re-expressed and made specific if they are to be used as measures of success. Thus, in the examples given above, the objective should be expanded by stating which species (e.g. *establish the following six species...*), what is meant by vegetation condition (e.g. *less than 30% cover is non-native*) and how much of an increase (e.g. a *three-fold increase*). Quantifiable objectives are also known as targets.

Set realistic objectives

Possibly the biggest challenge in setting objectives is to be realistic. Achievable and realistic are closelyrelated: but whereas achievable emphasises the resources needed, realistic refers to the biophysical limitations. It is not possible for an objective to be achievable or realistic without having considered threats and constraints, landscape context and future climate: these are emphasised in the guiding principles developed by Zedler (2000) (Appendix 2).

Setting realistic objectives means drawing on reviews such as this that summarise the state of knowledge about factors constraining recovery and about temporal considerations (Section 2.2). It also means deliberately working within biotic and abiotic constraints at the project site, if these cannot be removed or rectified. In cases where the abiotic characteristics have changed and cannot be reversed (for example, if the water regime has changed from intermittent to permanent, and water quality from fresh to brackish), then it is not realistic to aim to re-instate the pre-disturbance floristics. Wetlands that have changed irreversibly can be thought of as *novel ecosystems* (e.g. Hobbs et al. 2006) with *novel assemblages* of plant species. At such sites, the goal should be a vegetation type that is self-sustaining at that site under the altered environmental conditions.

Projects requiring decades (such as the establishment of a mature woodland or forest) may need to be managed as sequential shorter projects. In this example, the first recovery project objective should be to establish an earlier ecological stage (such as well-established saplings at an appropriate density).

Future needs: shifts in thinking

Objective setting has typically been at the scale of individual wetlands, with relatively little consideration about the wetland itself as part of a landscape-scale mosaic of wetlands. Advances in understanding the ecological significance of hydrological connectivity (Bornette et al. 1998, Greet et al. 2012, Morris 2012), dispersal mechanisms (Raulings et al. 2011, Soomers et al. 2013, O'Connell et al. 2013) and the role of refuges (Brock et al. 2003, Davis et al. 2013) mean there is a growing appreciation of how landscape-scale processes affect wetlands and their biota, and how an individual wetland contributes to this. Maintaining wetlands within a given landscape will mean setting priorities first at the landscape scale and then at the wetland-scale.

Priority-setting may also need to move away from restoring individual wetlands to thinking at a larger scale. Restoring a particular wetland or plant community may require considerable financial investment as well as a dedicated water allocation to provide a particular water regime, a situation that could poach resources from other wetlands in the region. In addition, criteria that have been conventionally used to evaluate importance might need to be modified. For example, nativeness, an attribute that features in most condition assessments, might need to be down-weighted in favour of attributes that refer to ecosystem functioning.

Principle 2: A recovery project should aim for vegetation at a wetland site to be self-sustaining, with opportunities for regeneration and establishment and renewal as required by the target vegetation.

For wetland vegetation to be self-sustaining, plant characteristics and requirements need to be matched to site conditions, especially to future water regime, future water quality and land management, and future climate. The conceptual framework summarises the factors and processes that determine Future Vegetation (box at right of Figure 5) at the site scale.

Practitioners can take this summary and make it specific to their wetland. Essential steps are first, to establish which of the three pathways connecting landscape to the wetland is having the most influence on vegetation dynamics, and second, to become familiar with the current vegetation and its ecological characteristics and recognise its requirements especially for regeneration. A key question here is to determine if the target vegetation is seed bank dependent or not.

Principle 3: A recovery project should plan how it will be documented so that the outcome and experience can be transferred and shared in the future.

It is not sensible for every recovery project to be documented to the same level of detail or to be treated as a research project. The level of detail needed will be determined partly by the complexity of the project itself, the resources required, and the level of uncertainty (i.e. ecological uncertainty) in meeting the objective; and this may be influenced by compliance and accountability requirements.

The absolute minimum is a one-page record of: site identity and initial characteristics; the long-term goal for the wetland as well as the project objective for vegetation recovery (if different); a record of management activities (what, when, where); and later, whether the project was successful, with notes as to why.

Future needs: Transferability

In their evaluation of restoration in Australia (Section 1.4.2), McDonald and Williams (2009) pointed out that it is not feasible to study every species or every site, therefore scientists need to find ways of transferring scientific results between regions and between species. This is transferability. It means understanding how abiotic drivers such as temperature and moisture determine species growth, germination and phenology; how these abiotic drivers vary across Australia; and how ecological strategies vary regionally. Currently there are several eco-regionalisations available, such as the Victorian-based wetland landscapes (DELWP 2016c), nation-wide system of bio-regions (IBRA), ecoregionalisation (Lechner et al. 2016) and empirical regionalisation (Hamilton et al. 2017). Which, if any, of these represents shared ecological traits and strategies among wetland plants has not been tested, but would be valuable to establish.

Current capacity to transfer knowledge is somewhat limited, as emphasised by some recent seed bank studies. For example, thermal stratification was needed for 4/9 plant species to germinate from the sediment seed bank of a seasonal wetland in Western Australia (Tuckett et al. 2010) but thermal stratification is not used when germinating sediment seed banks from seasonal wetlands in a similar climate in south-eastern Australia (e.g. Nicol et al. 2003). Similarly, Brock et al. (2005) found that sediments collected from major

wetland systems across the Murray-Darling Basin had differing responses to salinity and water regime: the authors were unable to resolve if this was due to disturbance legacy, recent history or natural variation.

Capacity-building can be done by investing in large-scale comparative studies, such as by Pettit and Froend (2001) on the relative importance of dispersal, serotiny, seed release and phenology for dominant riparian species on a tropical and temperate river system.

Contemporary knowledge about wetland plants is biased towards particular species, particular types of wetlands, and particular parts of Australia, a situation that has not changed much in fifteen years (Roberts 2001), despite considerable advances. Some examples of knowledge bias are: seed longevity is largely known from one study of species occurring in lagoons of the Northern Tablelands of NSW (Brock 2011), yet little is known of rhizome or root stock survival, even though this type of persistence applies to most rhizomatous clonally-growing species (*Typha, Phragmites, Eleocharis* spp.), many floodplain grasses (*Paspalidium jubiflorum, Paspalum distichum, Sporobolus spp, Pseudoraphis spinescens*) and perennials with annual or seasonal dieback or deciduous habit (*Duma florulenta*); seed bank studies are almost exclusively undertaken in temporary, seasonal or intermittent wetlands.

Capacity to transfer knowledge would help overcome geographic bias, as would a shift to using trait-based approaches in wetland plant species. Van der Valk's wetland sieve model (van der Valk 1981) used plant life history traits to predict regeneration responses to water regime. More recently Catford and Jansson (2014) and Purcell (2016), successfully used plant traits to understand the effects of regulation or clearing on species composition (e.g. Catford et al. 2014, Dawson et al. 2017). In the case of climate change, for example, it will be useful to develop response groups based on traits such as seed longevity in soil, mode(s) of dispersal, type of photosynthesis, as well as thermal tolerances of different life stages. Approaches to working with functional traits are being developed and applied (e.g. Catford et al. 2014, Dawson et al. 2017, Purcell 2016). The predictive value of particular plant traits will vary depending on the environmental conditions and the management outcomes being sought.

Principle 4: Time needs special consideration when planning a wetland vegetation recovery project, as several time-scales are relevant.

Time can be the most challenging part of wetland vegetation recovery. To be successful, a recovery project needs to combine different time-scales and mesh an anthropogenic view of time (calendar years, funding deadlines) with a time-frame appropriate for vegetation response (growing seasons, regeneration opportunities) and likely hydrology (inundations, draw-downs). Planners also need to be aware of trajectories (Section 3.5) and recovery rates (Section 2.2.2). There is no simple way to address these, other than being prepared with a contingency plan and building in flexibility.

Plants are perceived as straightforward part of wetland recovery but the evidence from meta-analyses shows that full recovery to a pre-impacted vegetation or reference plant community is slow and might not be achieved. This has several implications including uncertainty if this is an ecological bias (certain species, certain traits), and the definition of success (shifting the emphasis from full floristic recovery to other measures such as ecological function and ecosystem processes).

6.2 Planning vegetation recovery

This section describes a decision support tool (DST) that will improve the likelihood of success of a vegetation recovery project, followed by two options worth considering when deciding whether to take a passive or active approach, and then some general advice on strategies for dealing with a changing climate.

A decision support tool

It can be demanding to plan out all the steps in a recovery project, or to decide how best to prepare a recovery plan and be successful (i.e. to meet its objective). A decision support tool has been developed that will do this objectively based on the knowledge represented in this review. The tool is presented as a decision tree that asks a series of questions, first about the site, and then about the current vegetation at the site. Answers to the questions take the user to an evaluation of their planned approach, and provide some feedback, relative to their original objective. The paper version of this User Guide is in draft form (Roberts et al. 2017) and a digital version suitable for use on portable devices is scheduled.

Active and passive restoration

The condition of current vegetation (Figure 5) is an important consideration in planning wetland recovery, but determining the condition of the sediment seed bank is not straightforward. Currently, there are two ways of doing this. One is to establish a recent history of the site, and then use this to make assumptions about the

likely condition of the sediment seedbank (whether depauperate or not, whether weedy or not), using the knowledge summarised here in this review. The other is to do a seed bank trial.

Seed bank trials have been widely used by researchers and the techniques and protocols are now wellestablished. General advice on how to conduct a seed bank trial was drawn up more than twenty years ago (Brock et al. 1994). Despite the availability of this advice, there has been little inclination to test seed banks prior to restoration (Ficken and Menges 2013). Possible reasons are that seed bank testing is perceived as a research tool, and as being time-consuming, and is an additional cost. In addition, there could be uncertainty about how to process the information, and interpret the outcome, and how to relate this to the target vegetation. However, seed bank trials can be done by non-specialists, although expert advice with seedling identification may be needed. Guidance has been prepared (Brock 1997) so is available for those community groups that have the interest and commitment to do this themselves.

If a seed bank trials shows that sediment seed bank in the wetland is unlikely to support recovery, for example because it is depleted or depauperate or dominated by undesirable species, then seed bank material can be transferred from other suitable wetlands, known as *donor wetlands* (Brock 1997). This technique is sometimes referred to as *diaspore transfer* (Klimkowska et al. 2007), and it can be highly effective. In the case of degraded fen meadows in Poland, diaspore transfer was the only way to restore the vegetation (Klimkowska et al. 2010).

Strategies for recovery under climate change

Practical guidelines for plant restoration under a changing climate have been developed by Broadhurst et al. (2016). Although targeted at terrestrial systems, guidelines on sourcing material, genetic considerations, future seed availability and viability, and species selection are directly relevant to active restoration (planting) in a wetland recovery context.

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APPENDIX 1: Selection criteria for the 'Top 25'

The eight selection criteria used to select the top 25 restoration projects in Australasia, which were then showcased on the website of the Global Restoration Network are listed below. The criteria are based on the Primer developed by the Society for Ecological Restoration (2004), and were approved by the Council of the Ecological Society of Australia in 2008.

A project:

- 1 Is an outstanding Australasian example of ecological restoration for a particular biome or ecosystem
- 2 Has broken new ground in terms of ecological or on-ground philosophies or techniques
- 3 Is based on sound ecological principles and clearly stated goals
- 4 Exhibits high quality on-ground implementation standards
- 5 Has demonstrated results over many years
- 6 Is of a significant scale or with potential to be adopted on a larger scale
- 7 Has been soundly monitored and evaluated and has had at least one peer reviewed article published on it
- 8 Has sound social underpinnings and sufficient support to be sustained into the future.

The list of the 'Top 25' restoration projects recognised for Australia included five that were wetlands:

- · Watering wetlands on Murray floodplain private properties
- Alpine wetland restoration
- Sydney Olympic Parklands
- Kooragang Wetland recovery
- Clarence Valley Floodplain wetland project

Details can be accessed via the Global Restoration Network:

http://www.globalrestorationnetwork.org/countries/australianew-zealand/australia/

APPENDIX 2: Principles

Key principles of ecological restoration practice (from McDonald et al. 2016) http://www.seraustralasia.com/standards/contents.html

- Principle 1: Ecological restoration practice is based on appropriate local indigenous reference ecosystem.
- Principle 2: Restoration inputs will be dictated by level of resilience and degradation.
- Principle 3: Recovery of ecosystem attributes is facilitated by identifying clear targets, goals and objectives.
- Principle 4: Full recovery is the goal of ecological restoration but outcomes may take long timeframes.
- Principle 5: Restoration science and practice are synergistic.
- Principle 6: Social aspects are critical to successful ecological restoration.

Wetland restoration principles, from US EPA (2000)

https://www.epa.gov/wetlands/principles-wetland-restoration

- Preserve and protect aquatic resources
- Restore ecological integrity
- Restore natural structure
- Restore natural function
- Work within the watershed/landscape context
- Understand the potential of the watershed
- · Address ongoing causes of degradation
- Develop clear achievable and measurable goals
- Focus on feasibility
- Use reference sites
- Anticipate future changes
- Involve a multi-disciplinary team
- Design for self-sustainability
- Use passive restoration, when appropriate
- · Restore native species, avoid non-native species
- Use natural fixes and bioengineering
- · Monitor and adapt where changes are necessary

Ecological principles for wetland restoration, from Zedler (2000)

Ecological principles					
1	Landscape context and position are crucial				
2	Natural habitat types are the appropriate reference systems				
3	The specific hydrological regime is crucial to restoring biodiversity and function				
4	Ecosystem attributes develop at different paces				
5	Nutrient supply rates affect biodiversity recovery				
6	Specific disturbance regimes can increase species richness				
7	Seed banks and dispersal can limit recovery of plant species richness				
8	Environmental condition and life history traits must be considered when restoring biodiversity				
9	Predicting wetland restoration begins with succession theory				
10	Genotypes influence ecosystem structure and function				

Weinstein et al. (2001).

Principle 1:	State project goals clearly, as agreed to by the stakeholders: make the goals site-specific and realistic.
Principle 2:	Restore degraded sites rather than create new wetlands
Principle 3:	Select sites in a landscape ecology framework
Principle 4:	Ecological engineering practices should apply
Principle 5:	Restored sites should be self-sustaining, but should be 'guided' by adaptive management toward desired endpoints.
Principle 6:	Site monitoring should be planned and implemented, and last until success is assured.
Principle 7:	Success criteria should include functional as well as structural components (framed by a' bound of expectation')
Principle 8:	Consider people and property, a management plan should be developed that protects offsite elements
Principle 9:	Where possible, sites should be developed with conservation restrictions to ensure their perpetuity and to protect adjacent property.

Principle 10: Site plans should encourage public access for sustainable uses.

APPENDIX 3: Climate Change projections

Regionalised climate change projections

Changes in rainfall, extreme rainfall and drought, temperature and extreme temperature for Southern Australia, Eastern Australia, Northern Australia and Rangelands. Confidence ratings where available: M=medium, H=high, VH=very high (CSIRO and BOM 2015).

	Region (supercluster)					
	Southern Australia	Eastern Australia	Northern Australia	Rangelands		
Temperature	Continued substantial increases in mean, maximum and minimum temperatures (VH) In the near future (2030), annual average warming of 0.5 to 1.2 °C relative to 1986–2005 (mean of all CO ₂ scenarios) By 2090, annual average warming of 1.2 to 2.1 °C under an intermediate emission scenario and 2.7 to 4.2 °C under a high CO ₂ concentration scenario	Continued substantial increases in mean, maximum and minimum temperatures (VH) In the near future (2030), annual average warming of 0.5 to 1.4 °C above the climate of 1986–2005 (mean of all CO ₂ concentration scenarios) By 2090, annual average warming 1.3 to 2.6 °C under an intermediate CO ₂ concentration scenario and 2.8 to 5.0 °C under a high CO ₂ concentration scenario	Continued substantial increases in mean, maximum and minimum temperatures (VH) In the near future (2030), annual average warming of 0.5 to 1.3 °C above the climate of 1986–2005 (mean of all CO ₂ concentration scenarios) By 2090, annual average warming 1.3 to 2.6 °C under an intermediate CO ₂ concentration scenario and 2.7 to 4.9 °C under a high CO ₂ concentration scenario	Continued substantial increases in mean, maximum and minimum temperatures (VH) In the near future (2030), annual average warming of 0.6 to 1.4 °C above the climate of 1986–2005 (mean of all CO ₂ concentration scenarios) By 2090, annual average warming 1.3 to 2.6 °C under an intermediate CO ₂ concentration scenario and 2.7 to 4.9 °C under a high CO ₂ concentration scenario		
Extreme temperatures	Substantial increase in the temperature reached on hot days, frequency of hot days, and duration of warm spells (VH) Extreme temperatures increase at a similar rate to the mean temperature Frost-risk days (minimum temperatures under 2 °C) decrease (H)	Substantial increase in the temperature reached on hot days, frequency of hot days, and duration of warm spells (VH) Extreme temperatures increase at a similar rate as mean temperature Frost-risk days (minimum temperatures under 2 °C) decrease (H) Some areas could experience around two to three times the average number of days above 35 °C under intermediate CO ₂ concentration scenarios by late in the century	Substantial increase in the temperature reached on hot days, frequency of hot days, and duration of warm spells (VH) By 2090, Darwin and Broome could experience temperatures over 35 °C for a third of the year under an intermediate CO ₂ concentration scenario By 2090, Cairns could experience a 3-fold increase in days with temperatures over 35 °C under intermediate CO ₂ concentration scenario	Substantial increase in the temperature reached on hot days, frequency of hot days, and duration of warm spells (VH) By 2090, for Alice Springs, days with temperatures over 35 °C could occur for more than a third of the year under an intermediate CO ₂ concentration scenario Where frosts (minimum temperatures under 2 °C) occur in the cluster, these decrease.		
Rainfall	In the near future (2030), natural variability dominates changes, however a 15% decrease in	In the near future (2030), natural variability dominates any changes, however a decrease in winter and spring	Natural climate variability to remain the major driver of rainfall changes in the next few decades	For the near future, natural variability will dominate any changes		

	Region (supercluster)					
	Southern Australia	Eastern Australia	Northern Australia	Rangelands		
	winter and spring is predicted (M in Tasmania, H elsewhere) By 2090, decrease in winter of 20% (Victoria) and 25% (south- western Australia) under an intermediate CO ₂ concentration scenario and up to 30% (Victoria) and 45% (south- western Australia) under a high CO ₂ concentration scenario By 2090, an increase in winter rainfall in eastern Tasmania Continuation of observed autumn rainfall declines	is predicted (H) By 2090, decreasing winter rainfall inland (H) and south coastal (M) By 2090, decreasing rainfall in spring (M) Large uncertainty in the region related to the range of rainfall drivers and competing influences on rainfall change as well as their relationship to topographical features such as the Great Dividing Range and Eastern Seaboard	Changes to rainfall are possible but unclear By 2090, potential summer and autumn rainfall changes are approximately –20 to +10% under an intermediate emissions scenario and –30 to +25% under a high CO ₂ concentration scenario	Changes to summer rainfall are possible but unclear Winter rainfall decrease in the south (H)		
Extreme rainfall, drought, tropical cyclones	Increase in the time spent in drought over the course of the century (M) Increase in intensity of extreme rainfall events (H), (M – south west Western Australia)	Increase in intensity of extreme rainfall events (H)	Increase in intensity of extreme rainfall events (H) Tropical cyclones become less frequent, but the proportion of the most intense storms increase (M)	Increase in the time spent in drought over the course of the century (M) Increase in intensity of extreme rainfall events (H)		
Evaporation	Potential evapotranspiration increase in all seasons (H)	Potential evapotranspiration increase in all seasons (H)	Potential evapotranspiration increase in all seasons (H)	Potential evapotranspiration increase in all seasons (H)		
Fire weather	Harsher fire-weather climate in the future (H)	Harsher fire-weather climate in the future (H)	No change expected in fire frequency in regions with abundant rainfall (Top End, Kimberley, Wet Tropics) (H) In other locations, changes to future rainfall will be the determining factor of change to fire frequency When fire does occur, its behaviour will be more extreme (H)			
Solar radiation, humidity	An increase in solar radiation and a decrease in relative humidity in the cool season through the century (H)	Decline in humidity in winter and spring (H) and summer and autumn (M), though short term changes small.	By 2090, a decrease in humidity (M)	Increase in solar radiation in the south in winter (M) Decline in humidity in winter and spring (H) and summer and autumn (M), though short term changes small		

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