Managing natural resources for their human values

M. J. Smith,1,† P. L. Drake,1,2 R. Vogwill,3 and C. A. McCormick1

1Science and Conservation Division, Department of Parks and Wildlife, 17 Dick Perry Avenue, Technology Park, Kensington 6151 Australia
2School of Plant Biology, University of Western Australia, 35 Stirling Highway, Crawley 6009 Australia
3School of Earth and Environment, University of Western Australia, 35 Stirling Highway, Crawley 6009 Australia

Citation: Smith, M. J., P. L. Drake, R. Vogwill, and C. A. McCormick. 2015. Managing natural resources for their human values. Ecosphere 6(8):140. http://dx.doi.org/10.1890/ES15-00125.1

Abstract. Species composition and structure are important properties that can influence the extent to which people value a natural element. Hence these two properties can provide a means to directly manage natural elements to meet values-based goals. With this principle in mind, we studied soil seed bank assembly in two wetland vegetation elements recognized for their science/education, opportunity and system benefit values. Because seed banks drive the composition and structure associated with a vegetation element, which in turn influence human value satisfaction, variance partitioning modeling was used to determine which combination of filters best described patterns in the seed bank beta diversity. A combination of abiotic (soil permeability and soil salinity) and spatial filters with several interactions were the best descriptors of beta diversity, particularly for one vegetation element (wetland 1). Within the remaining vegetation element (wetland 2), a much greater diversity of weed species was observed. Based on the different patterns in diversity, including the links between these patterns, particular filters, and associated processes, we propose that the two vegetation elements, despite their close proximity to each other, are on diverging reassembly pathways. To manage the vegetation elements such that they maintain their values, we suggest hydrological processes are controlled to ensure that soil salinity does not increase dramatically. Dramatic increases in salinity will decrease element value by reducing vegetation diversity and plant community structure. We also stress the importance of understanding and managing processes that effect within-element dispersal and invasion by weeds. Here we demonstrate a general approach to inform the management of natural resources. It is important to identify, understand, and manage the filters (and associated processes) that restrict observable patterns in the properties that influence element value, sensu rules to manage the human valuation of natural elements.

Key words: beta diversity; ecological filters; human value; seed bank; threatening process; wetland vegetation.

Received 2 March 2015; revised 15 April 2015; accepted 21 April 2015; published 24 August 2015. Corresponding Editor: D. P. C. Peters.

Copyright © 2015 Smith et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited. http://creativecommons.org/licenses/by/3.0/
† E-mail: michael.smith@australianwildlife.org

INTRODUCTION

An important challenge for managers of natural resources, that we address in this paper, is to ensure system elements maintain their value to people (Keeney 1992, Wallace 2012). By element we mean any biotic or abiotic component of the system that is of value to people (e.g., a particular grouping of wildlife, a community of plants or a body of water). One important consideration is that elements can be described by their properties, such as species composition and structure in the case of a vegetation element, which influence or even determine the extent to which people value them (e.g., Ribe 2005, Shelby et al. 2005, Lindemann-Matthies et al. 2010, ...
Garcia-Llorente et al. 2011). Of note, properties are sometimes referred to as attributes or criteria by other authors (e.g., Pouwels et al. 2011) but we opt for the term properties throughout this paper. To manage element properties such as species composition and vegetation structure (in our case study we only consider vegetation elements) to meet value expectations, we must identify, understand and be able to control the processes that define the potential niche of certain taxa (Burgman 2005, Wallace 2012). A significant step towards achieving this goal will be to identify rules of assembly (Hobbs and Norton 2004) that can be related to processes that threaten the desired state of key element properties.

Vegetation elements can be thought of as being in a permanent state of change and re-assembly (Hobbs and Norton 2004). Following Götzberger et al. (2012) assembly rules are “restrictions on the observed patterns” due to ecological and phylogeographic filtering (in this paper we only assess ecological filters). Processes are the mechanisms that create these patterns. By assessing relationships between filters and patterns, assembly rules help us to characterize and classify the processes and interactions that influence the composition of species and the structure of elements in a given location. To occupy a site (presumably for some minimum time period), individuals from a regional pool of species must first arrive (dispersal filter) and then successfully establish themselves within the context of a set of biotic and abiotic filters and their interactions (Crawley 1996, Hobbs and Norton 2004). Management activities (i.e., weeding or hydrological control) may take effect at any level of this hierarchy (Booth and Swanton 2002).

In southwestern Australia, the location of this case study, wetlands of the semiarid zone are often remnant systems within a landscape that has been radically transformed by agricultural development and dryland salinity (Lyons et al. 2004). As in other parts of the world (e.g., Costanza et al. 1997), the wildlife associated with wetlands in southwestern Australia is valued by people for many different reasons (Davis and Froend 1999). Consistent with the definitions and classification of Wallace (2012), these values can include recreation, knowledge and heritage, philosophical/spiritual content-ment, adequate resources, health benefits, aesthetic enjoyment and opportunity (or future options). Refer to Wallace (2012) for a definition of human value as used in this context. A direct consequence of the degradation of many of the world’s wetland systems (Mitsch and Gosselink 2007), including those in southwestern Australia, will be a modified biological composition and vegetation structure which, in turn, will influence the wetland’s value to people (Chapin et al. 2000).

At any point in time, the species composition of a vegetation element will be intimately connected to the associated soil seed bank (Leck 1989). In combination with various filters in operation, the soil seed bank will shape the composition of future plant cohorts (Primack and Miao 1992, Capon and Brock 2006) and relate strongly to ecological assembly/reassembly (Poschlod et al. 2012). In this context, assembly rules will determine the seed bank beta diversity through filters that encourage (or discourage) seed arrival, germination, and subsequent plant growth (Leck and Simpson 1987). By influencing species diversity, these filters will affect the extent to which people value the element (Chapin et al. 2000, Schlacher et al. 2014). To demonstrate our thesis, we studied the rules of assembly relating to key threatening processes for seed bank beta diversity in two wetland vegetation elements. The two wetlands are affected differently by processes originating in the surrounding, highly disturbed landscape. Our aim was to examine the relationships between beta diversity (an established approach to quantifying biological composition; Legendre et al. 2005, Borcard et al. 2011) and two important threatening processes that were described by sets of ecological filters to facilitate management for human value. Although it is common to determine the extent to which beta diversity is influenced by dispersal-or ecological-constraints, (e.g., Crist et al. 2003, Chang et al. 2004, Legendre et al. 2005, Gianuca et al. 2013), it is rarer that such research links ecological process to the values people place on the system’s elements (e.g., Garcia-Llorente et al. 2011). Although a specific case study was used, the approach—which is essentially a framework to understand and then manage processes that threaten the properties that influence element value—should broadly apply to the management of natural resources.
METHODS

Study area

The case study was conducted in the Drummond Nature Reserve (Fig. 1), southwestern Australia. The reserve covers 4.39 km² of natural woodland and experiences a Mediterranean climate, with cool wet winters and hot dry summers. By natural, we mean elements that exist in nature, but are not produced or caused by people. Annual average rainfall from Bolgart (Bureau of Meteorology station number 010009, located 10 km northeast of the nature reserve) is 457 mm, with the majority falling between May and August when temperatures are lowest.

Geologically, the reserve is composed of lateritic ridges underlain by weathered Archaean granitic bedrock that forms part of the Yilgarn Craton (Carter and Lipple 1982). Like many locations in southwestern Australia, the regolith is composed of saprolite, overlain by clay which in turn is overlain by silcrete and laterite gravels.
on ridges. Parts of the reserve are dominated by sands, including the perimeters of two clay-based, ephemeral freshwater wetlands that are the subject of the present study (Forbes and Vogwill 2012). The vegetation of the wetlands, which are located in the northeast (wetland 1) and southwest (wetland 2) corners of the reserve (Fig. 1), is gazetted as a Threatened Ecological Community under Western Australian state legislation because of the presence of rare assemblages of natural perennial and annual plant species.

The canopy stratum of each wetland is almost exclusively occupied by dense stands of the paperbark shrub Melaleuca lateritia (A. Dietr.) with an understory of mostly annual herbs (Keighery et al. 2002). When the wetlands are inundated with water, they also support several aquatic plant species, including the gazetted Priority taxa Hydrocotyle lemnoides and Schoenus natans (Keighery et al. 2002). Wetland 2 is located within 100 m of the reserve boundary and as such is in close proximity to the adjacent agricultural land. In contrast, wetland 1 is more than 400 m from the boundary of the reserve and thus has a larger buffer of intact natural woodland compared to wetland 2 (Fig. 1).

The surface water hydrology of the wetlands also differ, with the catchment of wetland 2 extending well into the surrounding agricultural landscape, while over 90% of the catchment of wetland 1 resides within the boundary of the nature reserve. Despite these differences, both wetlands are usually inundated each year as a result of locally generated runoff. The wetlands are ephemeral (Chow et al. 2010, Forbes and Vogwill 2012) and are each approximately 0.03 km² in size. Maximum surface water depths in winter are around 50 cm (Forbes and Vogwill 2012). The aquifer beneath the wetlands is saline but, because of high depth to regional groundwater, water from this aquifer is unlikely to interact with the wetland root zone or surface water. Seasonally, a zone of saturation may occur in the wetland sediments as a perched aquifer (Forbes and Vogwill 2012).

**Human values**

The study catchment is managed under the recommendations of a publically available 20-year Recovery Plan (Department of Parks and Wildlife 2013). The plan can be accessed at http://www.dpaw.wa.gov.au/management/wetlands/264-natural-diversity-recovery-catchment-program. Two areas of information in the Recovery Plan that in particular relate to the present study are the identification of important human values relating to the system’s biological elements and a rating of processes that threaten the system’s elements. The biological elements under investigation in this study (the two wetland plant elements) have been identified as primarily providing three important, but potentially conflicting human values, in order of ranking: scientific/education values, system benefits values, and opportunity (or future options) values (Department of Parks and Wildlife 2013). As part of the catchment’s planning process, an advisory committee classified and ranked the important human values expected from the biological elements threatened by altered hydrology over a 20-year management period (2011–2031; Department of Parks and Wildlife 2013). The advisory committee, which included key communities of interest (e.g., agencies responsible for the management of biological diversity, water, and agriculture, and local communities groups), considered the biological elements at risk from altered hydrology and defined eight human values. The committee ranked the values in relation to the biological elements of interest and agreed that the top three ranked values should be the priority for management (Department of Parks and Wildlife 2013). The Recovery Plan states that (1) the scientific/education and opportunity values depend upon maintaining the current composition of natural plants over the management period and (2) the system benefits values relate to the management of hydrological processes in the surrounding catchment in order to mitigate against adverse downstream effects associated with flooding and the excessive movement of water borne threats such as nutrient runoff (Department of Parks and Wildlife 2013). The links between element diversity and the attainment of the priority values are deliberated upon further in the Discussion.

The current structure of the wetland vegetation elements is strongly linked to the presence of *M. lateritia* (the shrub species that dominates the canopy overstory) and an understory composed
of annual herbs and aquatic plants. Vegetation structure, in this context, can be thought of as the three-dimensional distribution of plant biomass which will govern each wetland’s capacity to mitigate the adverse effects of flooding and transport of soil borne threats. The provision of system benefits will be dependent on maintaining the overstory of *M. lateritia* while ensuring that the overall volume of live plant biomass in the understory is not significantly diminished. The loss of some of the herbs or aquatic plants (depending on the species) may not decrease the wetland’s system benefits values.

**Threats**

As part of the catchment’s planning process, an expert analysis of the probability that a set of threatening processes would cause management goal failure was conducted by an advisory group who identified altered hydrology and environmental weeds as the two most important threatening processes in terms of managing the biological elements associated with the wetlands (Department of Parks and Wildlife 2013). Following Arcioni (2004), we consider environmental weeds to be plants that are detrimental to natural flora and fauna and that weeds are plants growing where they are not wanted.

As detailed in the catchment’s Recovery Plan, the threat analysis was a desktop exercise based around the approaches outlined by Wallace et al. (2003), Walshe (2005), and Walshe et al. (2007). Threats associated with nutrient cycles, fire regime, and human attitudes were also seen to be important, in that order (Department of Parks and Wildlife 2013). We build our assembly rules around the two most important threats, hydrology, and environmental weeds, as they were considered to be priorities for managing the natural composition of the wetland biological elements such that the key values are maintained over the management period (20 years); as outlined in the Recovery Plan (Department of Parks and Wildlife 2013). Thus, some processes threaten element properties that influence the values that people place on the biological elements of interest.

To assess assembly rules, we incorporated these two threatening processes into variance partitioning analyses (Borcard et al. 2011), by identifying relevant and measureable biotic and abiotic filters. The biotic filters were taken to be the abundance of weeds and *M. lateritia* canopy cover. The abiotic filters were soil salinity, soil moisture, soil type, and site elevation. The selected filters relate to direct or near direct risk factors (Metcalf and Wallace 2013). For example, water quality and quantity are abiotic filters that present direct risks to the survival and reproduction of plants via mortality associated with salt toxicity or drought stress. These filters were quantified by measuring soil salinity, soil moisture, soil type, and elevation. The near direct risk presented by weeds (direct risk factor would be something like competition for nutrients or light resources) was quantified by calculating weed abundance.

**Sampling sites**

Forty randomly assigned sites were established in wetland 1 and 39 in wetland 2 (Fig. 1) in February 2012 and the experiment proceeded until December 2013. All subsequent methodologies are referenced to these sites.

**Soil seed bank**

From each site five soil samples were obtained from within a 1 × 1 m area in June 2012. Soil samples were collected in a random spatial pattern using a steel pipe (internal diameter = 5 cm) which was inserted to a depth of 5 cm from the soil surface. Soil samples were aggregated to the site level then divided in two, with half of the soil used to characterize the soil seed bank and the remaining half used to determine soil moisture content, soil salinity, and soil type. To characterize the soil seed bank at each site, we filled plastic trays with soil to a depth of 10 mm. The trays had the dimensions 165 × 115 × 50 mm, and holes were drilled in the base of each tray to allow water to drain. The trays were then positioned on a bench in a glasshouse in a randomized pattern and watered for 20 s at 20-min intervals using misting sprinklers during the day and 20 s every hour at night. A heat mat, set to 20°C, was used to regulate the temperature of soil and air temperature was controlled by two evaporative air conditioners. We monitored soil and air temperature at hourly intervals using two iButton temperature sensors (Model DS1921G, Maxim Integrated, San Jose, California, USA), which recorded a temperature range of 5.0–
35.0°C and 5.5–34.5°C for soil and air temperatures, respectively. The sensor assigned to measure soil temperature was positioned on the soil surface of a tray whereas the sensor allocated to measure air temperature was suspended from a cable approximately 3 m from the trays.

After approximately five months, the number of plants emerging from soil ceased so the experiment was terminated. At this stage the abundance of each different taxon was determined for every tray. Note that because of the size and/or stage of maturity of individuals, we were unable to identify all plants to the species level (Appendix A). We considered that the plants emerging from each tray represented the diversity of the seed bank at each site, although we acknowledge that our design was biased towards species that were adapted to germinating in moist conditions. Although our experimental approach may not have completely exhausted the soil seed bank, our objective was to provide a realistic measure of the beta diversity that would arise under natural conditions rather than an absolute measure of the seed bank beta diversity.

Referring forward to the Results section, *M. lateritia*, which dominated the overstory, was not represented in the soil seed bank of either wetland. Given its perceived importance to the human values of the wetlands, we undertook further experiments to determine whether the soil that was collected could sustain this species. The initial experiment described above was repeated, but included a treatment where approximately 1000 *M. lateritia* seeds (by weight) were added to the soil. Soil samples, using the methods described above, were collected in August from ten randomly selected sites per wetland (*n* = 5 soil samples per site). The soil was aggregated to the wetland level and mixed. Prior to adding seed, half of the soil from each wetland was sterilized using an autoclave (S.W. Hart & Co, Perth, Western Australia, Australia); sterilization at 67 newtons and 121°C for 21 min). The autoclaved treatment served to test whether a biotic element such as a pathogen or seed bank competitor limited the germination of *M. lateritia*.

For each wetland, a matrix of treatments was set up as follows: (1) not sterilized, no seed added, (2) not sterilized, seed added, (3) sterilized, no seed added, and (4) sterilized, seed added. The added seed was obtained from mature capsules that were collected from the wetlands coincident with soil sampling. Capsules were placed in a controlled temperature facility set to an air temperature of 15°C and a relative humidity of 15% for 7 d in order to encourage dehiscence. A sample of seed (*n* = 200) was then germinated on agar in Petri dishes under the following conditions: 15°C and a 12 h light/dark photoperiod. This trial indicated that 48% of the seed released from capsules was viable. As with the previous experiment, we filled plastic trays with 1 cm of soil (*n* = 5 trays per treatment). The trays were then placed in a random spatial pattern on a bench in the same glasshouse. The watering regime and environmental conditions were the same as described previously. The experiment proceeded until the emergence of plants had ceased (after approximately five months). At this stage, we determined the total number of *M. lateritia* seedlings that emerged from the soil and also counted the number of additional seedlings that were present.

**Abiotic filters**

**Soil properties: salinity and moisture.**—On three occasions during 2012 the soil volumetric water content (*θv, %*) was determined in the field with a soil moisture meter (Model MP 406, ICT International, Armidale, New South Wales, Australia) employing the standing wave principle of measurement. These measurement occasions are referred to as the first reading, second reading, and third reading for 11 May, 23 May, and 13 November respectively. The three consecutive measurements of *θv* occurred prior to a fill event (first reading), just after the fill event (second reading), and after the fill water had receded (third reading). The duration and extent of the fill event that occurred during the study period was a typical hydrological cycle for the wetlands (Forbes and Vogwill 2012). For each measurement period, *θv* was determined at five random locations within a 1-m quadrat at each site. We used the generic soil calibration factor supplied with the moisture meter, which has a measurement accuracy of ±5% of *θv*.

After allocating half of each soil sample to the seed germination trial (see Soil seed bank), we further subdivided the soil into three equal portions, with each portion used to determine
the soil gravimetric water content ($\theta_g$), the soil electrical conductivity (EC), and the soil type, respectively.

For soil samples, $\theta_g$ (%) was determined as described above, according to $\theta_g = ((FW - DW)/FW) \times 100$. FW (g) is the fresh weight of soil and DW (g) is the dry weight of soil. Dry weights were obtained by oven drying soil at 105°C for 48 h. Before determining DW, soils were allowed to equilibrate to ambient air temperature in a desiccator.

The soil electrical conductivity was estimated from a 1:5 soil:deionized water suspension. Soil samples were air dried and sieved through a 2-mm mesh to remove large pieces of organic matter (plant detritus). For each sample a 1:5 soil:deionized water suspension was then measured out by weight (10 g of soil) and volume (50 ml of deionized water). Each suspension was then thoroughly mixed for 1 h using a mechanical shaker. The electrical conductivity of the 1:5 suspension (EC$_{1:5}$, $\mu$S cm$^{-1}$) was then measured with a conductivity meter (model LF 318, Wissenschaftlich-Technische, Weilheim, Germany). Data were then converted to the electrical conductivity of a saturated paste extract (EC$_e$, $\mu$S cm$^{-1}$) according to George and Wren (1985).

**Soil type.**—Soil type was determined following the methods of McDonald et al. (1990). A small subsample of soil (~2 cm$^3$) was taken from each sample (as outlined above). Each sample was moistened with water, a little at a time, and kneaded into a ball until it just failed to stick (to fingers), i.e., the sticky point was obtained. The soil ball (bolus) was kneaded for 1–2 min or until there was no apparent change in consistency. The bolus was then manipulated by forming a ribbon and shearing induced by pressing out the soil between forefinger and thumb. The behavior of the moist bolus and length of the ribbon during shearing was used to characterize the field texture. Wet hue was estimated from moist soil using a Munsell color system.

**Elevation.**—The elevation of each site was calculated as the absolute difference between the height of the nearest 0.25-m contour (from a contour GIS layer; EPSG:28350–GDA94/MGA zone 50) and the overall highest contour for the wetland. Calculations were conducted in ESRI ArcMap (version 10.1; Redlands, California, USA).

**Biotic filters**

**Canopy cover.**—For both wetlands, the overstory canopy was less than 3 m from the ground surface. We used nadir photography (Macfarlane and Ogden 2012) to quantify canopy cover in May 2012 at each site. Briefly, nadir images of the canopy were captured with a Nikon D7000 DSLR camera fitted with an AF-S Nikkor 24–120 mm lens (Nikon Corporation, Otowara, Tochigi, Japan). The lens was set to F11 and the camera operated in aperture priority mode. Images were taken using autofocus, auto white balance, and fine picture quality. Images were obtained using the sRGB color space and saved as both JPG and NEF formats. As with Macfarlane and Ogden (2012), the camera was attached to an extendable aluminum pole using an angled bracket to ensure that the camera faced straight down when images were captured. A bubble level was used to make certain that the correct plane was obtained before capturing each image. The camera was 4 m above the ground surface when images were captured, resulting in a field-of-view at the ground surface of 6.48 m$^2$. The camera was operated with an infrared remote control (model ML-L3) set with a 2 s delay. At every site an image was captured from each cardinal point resulting in four images per location.

We define the living canopy as that fraction of the overstory that is comprised of green leaves. In our study, the canopy was almost exclusively composed of *M. lateritia*. Accordingly, the metrics of canopy cover presented in this study represent the living extent of this species at the site. To determine the most appropriate canopy classification method, we used a random subset of 320 images from which we determined canopy cover by manually thresholding the hue, saturation, and brightness of each image until canopy pixels were separated from non-canopy pixels. Canopy cover was then calculated as the quotient of the number of canopy pixels to the total number of pixels in the image (termed manual canopy; Cm). This procedure was carried out in Image J, version 1.47t (Schneider et al. 2012). We then applied six automated classification methods to the same images using MATLAB version R2012B (Mathworks, Natick, Massachusetts, USA) following the protocol of Macfarlane and Ogden (2012). By regressing Cm with the canopy cover obtained by the automated classification methods, we determined that a histogram corner
detection algorithm (Rosin; Cr) was the best predictor of canopy cover: Cr = 1.16 Cm, \( R^2 = 0.930, P < 0.001 \). We subsequently used the Rosin algorithm and the relationship between Cr and Cm to calculate the canopy cover of the remaining images. Our estimated canopy cover does not account for the fraction of the canopy that is obscured by leaves or woody biomass when images were captured but given that most of the leaves were positioned on distal branches, this component of the canopy is likely to be very low.

Weed species.—Interactions with weed plant species were thought likely to be representative of an important biotic filter for the natural plant species. Consequently, the abundance of each weed plant species was recorded for each study site. To incorporate the effects of weed plant species (as a biotic filter), the abundance of each individual species was included as an independent variables in each analysis.

Spatial filters
A GPS was used to capture the geographical coordinates (Projected Coordinate System, GDA94 MGA Zone 50; Projection, Transverse Mercator) of each sample site. Following the approach outlined in detail by Borcard et al. (2011), a set of spatial descriptor variables were generated from each wetland’s geographical coordinates using principal coordinates of neighbor matrices (PCNM: a special case of Moran’s eigenvector mapping; Dray et al. 2006). The PCNM analysis produces a series of variables that capture the spatial variability (across all relevant scales) among the sample sites. The PCNM variables represent a gradient from the broadest (first variable) to the finest (last variable) spatial patterns.

The PCNM approach progresses by calculating a truncated Euclidean distance matrix from the geographical coordinates of the sites followed by principal coordinates analysis to calculate eigenvectors that are associated with the positive eigenvalues. PCNM variables were generated for each wetland independently.

Additional statistical analyses
Reducing the number of explanatory variables.—To avoid type I errors and to minimize overestimating the amount of explained variance in the species abundance matrices, forward selection with the Blanchet et al. (2008) double stopping criterion was applied to each set of explanatory variables (abiotic filters, biotic filters, and spatial dispersal filters) for each wetland. For each set of filter variables, a global redundancy analysis (RDA) was initially run with all explanatory variables. Adjusted \( R^2_{(Y|X)adj} \) was calculated for the global model using the Ezekiel’s correction (Peres-Neto et al. 2006), which was used with the alpha value (0.05) to select explanatory variables for a reduced analysis.

The forward selection routine starts by selecting variables to maximize the model fit and computing an \( F \)-ratio. A \( P \)-value permuted from the residuals is generated and \( R^2_{(Y|X)adj} \) for the forward test is computed when a \( P \)-value is \( \leq 0.05 \). When the \( R^2_{(Y|X)adj} \) of the test is lower than the global \( R^2_{(Y|X)adj} \), a new variable is added and the permutation test repeated. When the \( R^2_{(Y|X)adj} \) is higher the procedure is stopped.

Variation partitioning of the biotic, abiotic and dispersal filters.—Using the approach detailed by Borcard et al. (2011) variation in beta diversity was partitioned into several explanatory components; specifically the biotic component, abiotic component and two spatial components (e.g., broad and moderate) using the forward-selected data sets. Thus, variation in beta diversity was decomposed into pure abiotic filters, pure biotic filters, pure spatial dispersal filters, all combinations of these effects, and unexplained causes of variation. Refer to Borcard et al. (2011) for a very detailed and readable description of this analytical approach.

All analyses used in this paper were performed in R (version 3.0.2; R Development Core Team 2012). Species data matrices were Hellinger-transformed before inclusion in each analysis (Borcard et al. 2011). All continuous predictor variables were standardized to a mean of 0 and standard deviation of 1. Dummy variables were created for the soil type variable.

Results
Natural diversity
Thirty-one natural plant species emerged from the soil samples across the two wetlands. In their survey of mature plants in the same area, Keighery et al. (2002) found 67 natural species
in the Drummond claypans. Appendix A provides complete lists of the natural species found in both our experiment and in the survey of Keighery et al. (2002). We detected eight natural species not detected by Keighery et al. (2002; Appendix A). Twenty-three species were recorded in wetland 2 and 25 in wetland 1.

**General description of the biotic and abiotic filters**

In total, five weed species were recorded (Appendix A). All five species were present in wetland 2, whilst *Crassula natans* was the only weed species detected in wetland 1. Two of the weed species detected in this study were not detected by Keighery et al. (2002). Two were detected by Keighery et al. (2002) in the surrounding woodlands, but not in the claypans.

Most noticeably, on average wetland 1 had higher \( \theta_v \), \( \theta_r \), (second and third readings) and EC\( e \) (Table 1). Wetland 1 was characterized by more fine-grained soil samples (clayey and silty) compared to the coarser grained soil of wetland 2 (i.e., sandy and loamy; Table 2). The two wetlands had a similar range in relative elevation and had similarly dense canopies of *M. lateritia* (Table 1).

**Variation partitioning—wetland 1**

Forward selection of the biotic variables for wetland 1 (accounting for the alpha value of 0.05) produced a reduced set \( (R^2_{Y\vert X_{adj}} = 0.115, P < 0.01) \) that included canopy cover only. Forward selection of the abiotic variables for wetland 1 (accounting for the alpha value of 0.05) produced a reduced set \( (R^2_{Y\vert X_{adj}} = 0.276, P < 0.01) \) that included, in order of importance, EC\( e \), elevation, and \( \theta_r \), third reading (Fig. 2).

The PCNM analysis for wetland 1 produced 14 positive spatial variables. Forward selection of these 14 spatial descriptor variables (accounting for the alpha value of 0.05) produced a reduced set \( (R^2_{Y\vert X_{adj}} = 0.279, P < 0.01) \) of six variables that included, in order of importance, PCNM1, PCNM4, PCNM5, PCNM2, PCNM9, and PCNM6 (Fig. 3; Appendix B). For the variance partitioning analysis, and based upon the figures provided in Appendix B, the spatial descriptors were divided into two groups, broad scale spatial structuring (PCNM1 and PCNM2) and moderate to fine scale spatial structuring (PCNM4, 5, 6, and 9). Of particular note, spatial descriptor PCNM1 can be interpreted as representing a compositional transition from shoreline to the center of the wetland and spatial descriptor PCNM2 grouped diversity into a northern cluster and a southern cluster (Appendix B). With respect to the spatial variables, linear regression analysis showed that significant variation in PCNM1 \( (R^2_{Y\vert X_{adj}} = 0.69, F_{4.35} = 20.68, P < 0.01) \) was explained by canopy cover (slope = 0.59; \( P < 0.001 \)) and that significant variation in PCNM4 \( (R^2_{Y\vert X_{adj}} = 0.24, F_{4.35} = 3.97, P < 0.01) \) was explained by canopy cover (slope = 0.43, \( P < 0.01 \)) and the third \( \theta_v \) reading (slope = -0.44, \( P < 0.05 \)).

For wetland 1, 33\% of the variation was explained by the explanatory variables (ergo, 67\% remained unexplained; Fig. 4). Overall the

### Table 1. Average estimates (and SD) for each measured environmental variable in each wetland.

| Variable                  | Wetland 1  | Wetland 2  |
|---------------------------|------------|------------|
| Canopy (%)                | 16.99 (9.31)| 17.01 (9.93)|
| \( \theta_v \) (%)        | 9.31 (6.21)| 14.55 (6.86)|
| EC\( e \) \( (\mu S \ cm^{-1}) \) | 619.45 (376.52)| 428.95 (340.17)|
| Wet hue                   | 2.63 (0.48)| 3.03 (0.41)|
| \( \theta_r \), first reading (%) | 4.10 (4.49)| 14.44 (6.90)|
| \( \theta_r \), second reading (%) | 41.86 (15.37)| 30.13 (13.74)|
| Diversity weed species    | 0.08 (0.27)| 1.31 (2.72)|
| Elevation (m)             | 0.43 (0.13)| 0.39 (0.16)|

Notes: Environmental variables are as follows: percentage of canopy cover attributed to *M. lateritia* (canopy), gravimetric soil moisture content \( (\theta_v) \), the color of moist soil (wet hue), the volumetric water content measured in the field using a moisture meter prior to (\( \theta_r \), first reading), during (\( \theta_r \), second reading) and after (\( \theta_r \), third reading) filling, the diversity of weed species (Div weed sp.), and the relative elevation (elevation). For wetland 1, diversity of wetland species is abundance of *Crassula natans*. For wetland 2, diversity of wetland species is Shannon’s diversity index calculated from the abundances of the five weed species recorded at each site.

### Table 2. The number of study sites in each wetland characterized by each soil type.

| Soil types      | Wetland 1 | Wetland 2 |
|-----------------|-----------|-----------|
| Clay            | 0         | 4         |
| Clay loam       | 10        | 4         |
| Clayey sand     | 3         | 1         |
| Silty clay loam | 3         | 1         |
| Silty loam      | 3         | 0         |
| Loam            | 0         | 2         |
| Sandy clay loam | 9         | 3         |
| Loamy sand      | 6 (12)    | 9 (12)    |
| Sandy loam      | 6 (9)     | 9 (9)     |
| Sand            | 0         | 3         |
abiotic and the fine to moderate scale spatial filters were significant (abiotic, $F = 1.63$, $P < 0.05$; moderate to fine scale, $F = 1.92$, $P < 0.01$). The biotic and broad scale spatial filters were not significant (biotic, $F = 0.89$, $P = 0.53$; broad scale, $F = 1.51$, $P < 0.11$). Thus, the greater part of variation in beta diversity was explained by abiotic filters and moderate to fine scale spatial filters and can be summarized as

1) a pure moderate to fine scale spatial filter (7%).

2) a pure abiotic filter (4%) specifically relating to soil salinity, elevation and soil moisture. The abiotic filter interacted with:
   a) the biotic filter (canopy cover; 4%),
   b) the broad spatial filter (4%), and
   c) a three-way interaction with the broad spatial filter and the biotic filter (11%).

Fig. 2. Reduced environmental filtering RDA triplots of Hellinger-transformed wetland species data constrained by the spatial descriptors (fitted site scores (linear combination of explanatory variables)) for (A) wetland 1 and (B) wetland 2. Scale is 2. Numbers indicate site number. M dru is Myriophyllum drummondii, Aann is Apium annuum, Ste1 is sterile sp. 1, Sdes is Stylidium despectum, Unk is unidentified species, Bdr is Blennospora drummondii, Gpub is Grattiola pubescens, Cari is Cen tralepis aristata, Casp1 is Calandrinia sp., and Cexs is Crassula exserta.
Variation partitioning—wetland 2

Forward selection of the biotic filter variables for wetland 2 (accounting for the alpha value of 0.05) produced a reduced set ($R^2_{Y|X|adj} = 0.101, P < 0.05$) that included canopy cover only. Forward selection of the abiotic filter variables for wetland 2 (accounting for the alpha value of 0.05) produced a reduced set of variables ($R^2_{Y|X|adj} = 0.175, P < 0.02$) that included, in order of importance $\theta_v$ first reading, the sandy loam soil type, and $\theta_v$ third reading (Fig. 2).

The PCNM analysis for wetland 2 produced 14 positive spatial variables. Forward selection of these 14 spatial descriptor variables (accounting for the alpha value of 0.05) produced a reduced set ($R^2_{Y|X|adj} = 0.130, P < 0.05$) of two variables that included, in order of importance, PCNM1 and PCNM5 (Fig. 3). Thus, the significant PCNM variables related to broad (PCNM1) and moderate (PCNM5) scale spatial filtering (Appendix B).

For the variance partitioning analysis, and based upon the figures provided in Appendix B, the spatial descriptors were divided into two groups: broad scale spatial filtering (PCNM1) and moderate scale spatial filtering (PCNM5). Of note, spatial descriptor PCNM1 represented a compositional transition from the northeast to the southwest of the wetland (Appendix B).
of the biotic or abiotic variables explained
significant variation in the reduced set of PCNM
variables for wetland 2.
Only 19\% of the variation in the beta diversity
of wetland 2 was explained by the filters
(accordingly, 81\% remained unexplained; Fig.

4). Overall the abiotic and the broad spatial scale
filters were significant (abiotic, $F = 1.84$, $P < 0.05$;
broad scale, $F = 3.72$, $P < 0.001$). The biotic and
moderate spatial scale filters were not significant
(biotic, $F = 0.99$, $P = 0.51$; moderate scale, $F = 0.59$,
$P = 0.80$). Thus, the greater part of variation in
beta diversity that was explained could be
attributed to an abiotic filter and the broad scale
spatial filter and can be summarized as

1) a pure broad scale spatial component (7\%),
and
2) a pure abiotic component (6\%) specifically
relating to sandy loam soils and soil moisture.

**Experiment 2: M. lateritia seedlings**

Only one individual *M. lateritia* seedling
emerged from the non-seed treatments (in a
wetland 2 sample). Numerous seeds germinated
in the seeded samples (mean $= 20$, SD $= 11.6$). We
therefore concluded that the experimental condi-
tions were satisfactory for germination by *M.
lateritia* and that there were little to no viable
*M. lateritia* seeds present in the experimental soil
samples.

A Poisson generalized linear mixed-model
was used to assess the differences in *M. lateritia*
germination among the seeded autoclave
and wetland treatments (Table 3; note, residuals
appeared to exhibit normality, independence,
and homogeneity). Although there tended to be
fewer seedlings in the autoclaved treatments, the
effect was not significant (Table 3). However,
significantly fewer seedlings germinated in the
wetland 2 samples when compared to the
wetland 1 samples (Table 3).

---

**Table 3.** Results of a Poisson generalized linear mixed-
model (*M. lateritia* abundance $\sim$ autoclaved \times
wetland) of variation in *M. lateritia* abundance
explained by the autoclaved (yes or no) treatment
and the wetland (1 or 2) treatment.

| Coefficients                | Estimate | SE   | $t$     | $Pr(>|t|)$ |
|----------------------------|----------|------|---------|------------|
| Intercept                  | $3.490$  | $0.078$ | $44.699$ | $<0.001$   |
| Autoclaved                 | $-0.144$ | $0.115$ | $-1.257$ | $0.209$    |
| Wetland                    | $-1.111$ | $0.157$ | $-7.080$ | $<0.001$   |
| Autoclaved $\times$ wetland | $-0.156$ | $0.238$ | $-0.656$ | $0.512$    |

*Notes:* Minimum deviance residuals $= -1.457$ and maximum $= 1.215$ (first quartile $= -0.440$, median $= 0.074$, third quartile $= 0.367$). Null deviance $= 132.674$ (df $= 19$) and residual deviance $= 10.679$ (df $= 16$).
DISCUSSION

Identifying rules of ecological assembly by relating biotic and abiotic filters to patterns in biological composition can be an important step towards successfully managing the human value of natural living resources. The species that occupy an area will reflect filtering of the regional species pool by dispersal and ecological constraints (Götzenberger et al. 2012). In our study of patterns in the beta diversity of seed banks in two similar wetlands, we found differences in the significance of several filters (that relate to important threatening processes) and their interactions. We discuss these patterns within the context of ecological assembly in order to implement management for human value. Our basic premise is that the extent to which people value an element can be influenced by key properties such as species diversity. To manage elements for their value (i.e., Millennium Ecosystem Assessment 2005, Wallace 2012) an important step will be to relate patterns in key properties (i.e., species composition) to filters and their underlying processes. Assembly rules, which can be thought of as “restrictions to observed patterns” (Götzenberger et al. 2012), are thus identified. In this context, management activities can be thought of as filters themselves that affect system reassembly (Booth and Swanton 2002).

The links between biological element properties and the value people place on natural elements is still an area of active investigation. As such, some readers may question the links proposed here between structure and species diversity and the attainment of science/education, future opportunity, and system benefit value. Accordingly, we provide some additional justification. First, we do not imply that these relationships are simple, as they are likely to be very complex and subject to a variety of feedbacks and external processes that are beyond our scope. However, at a bare minimum there is ample evidence to suggest that there is a positive relationship between maintaining the natural diversity of specified elements and the attainment of both science/education value (Dudgeon et al. 2006) and future opportunity value (Chapin et al. 2000). Fig. 5 provides an example of the

![Fig. 5. Example of two closely situated wetlands (~4 km apart) in the wheatbelt region of Western Australia. The effects of secondary salinization are readily apparent in wetland (A; photo courtesy of Ray McKnight), whereas management intervention has resulted in the persistence of vegetation in wetland (B).](image)
effects of increasing salinity on wetland vegetation diversity and structure. From this figure, it is clear that the kinds of values associated with the study wetlands would be lost with a similar transition. The Convention on Biological Diversity (United Nations 1992) makes it very clear that biological diversity has scientific, education and future opportunity value and thus, a loss of natural diversity must mean some loss of those values. Chapin et al. (2000) eloquently summarizes the positive link between two of the key values that are relevant to the current study and species diversity (although they specifically refer to species extinction) with their comment that “the loss of a species to extinction is of special societal concern, however, because it is irreversible. Future opportunities to learn and derive newly recognized benefits from an extinct species are lost forever. Preventing such a loss preserves an ‘option value’ for society—the value of attaining more knowledge about species and their contribution to human well-being in order to make informed decisions in the future.” As an additional example, within the context of increasing exotic species diversity (which is very relevant to the present study), Sax and Gaines (2003) argued that the potential for education and the attainment of knowledge can depend upon maintaining natural species diversity in an invaded system. Charles and Dukes (2007) state that educational values are lost when species (they are referring to natural species) are lost from a system as a consequence of invasion by exotic species. There are also long established links between the persistence of natural species diversity and the attainment and dissemination of indigenous knowledge and associated education (e.g., Gadgil 1992, Brosi et al. 2007).

The link between aquatic vegetation structure (as a collection of functional traits) and water regulation and purification is clear (Turner et al. 2000, Bouldina et al. 2004, Brauman et al. 2007, Garcia-Llorente et al. 2011) and is recognized as important by the American EPA http://water.epa.gov/type/wetlands/flood.cfm. Thus, given that the wetlands of this study may, during wetter periods, connect hydrologically to downstream ecosystems, the structure of the vegetation communities was seen by the Recovery Plan advisory group to be closely linked to system benefit values (Department of Parks and Wildlife 2013) and a loss of structure would result in a loss of system benefit value. Collectively however, the previous two paragraphs do highlight that an important area for new research is to better qualify and quantify the actual relationships between element properties and the values to which they pertain. This will allow natural resource managers to better explain, justify, and monitor the effectiveness of their activities.

Even though the two wetlands had similar overall species richness, we detected differences in the distribution patterns of seed bank beta diversity and in the strength of the relationships between beta diversity and the studied filters. The degree of filtering and the degree of among-filter interaction was more pronounced in wetland 1, which was characterized by finer-grained surficial soils and higher soil salinity concentrations. Taking into account the similarity of the two wetlands in terms of their canopy cover and elevation, we propose one key rule for the two wetlands: soil type influences the accumulation of salts (e.g., Quirk et al. 1986), and through interactions with elevation, canopy cover, and soil moisture, soil type will effect beta diversity and thus, element value. Bearing in mind the differing patterning in the diversity of the two elements, our results may also align with Rule and Mechanism (9) of Belyea and Lancaster (1999) that “non-random spatial patterns of communities tend to develop due to positive feedback involving local alteration of environmental constraints.” Although we lack a detailed understanding of the chemical composition of the soil supporting the elements, general rules linking salinity to the shrinking and swelling of clay particles and soil bulk density (Shainberg and Letey 1984) highlight the potential for feedbacks between salinization and soil permeability.

Water and salt stress have profound effects on plant survival (Ladiges et al. 1981, Munns and Termaat 1986, Munns 2002, Carter et al. 2006, Salter et al. 2008) and species composition (James et al. 2003, Nielsen et al. 2003, Smith et al. 2009). Importantly, the nature of the relationship between plant survival and species composition with increasing salinization often conforms to a sigmoidal model (Carpenter 2003, Davis et al. 2003). Relatively small increases in salinity may result in dramatic changes in diversity when salt
concentrations are in the steep gradient of the sigmoid (Scheffer et al. 2001, Morris et al. 2003, Scheffer and Carpenter 2003). Based upon the proposed property–value relationship, this will lead to significant loss of the key values. By way of example, Nielsen et al. (2003) noted that electrical conductivities of standing water in excess of around 1500 $\mu$S cm$^{-1}$ were likely to cause significant mortality in wetland biota. Key management interventions may be undertaken if such thresholds are known and their mechanistic link to ecological filters has been established. Although our study design does not specifically address thresholds, we highlight one mechanistic link: the potential for increased salinization where soil permeability is low. Wetland salinization is a truly global issue (Vengosh 2014) and if not managed, increases in salinity will cause a loss of natural species and vegetation structure (Hart et al. 1991) including subsequent element value (e.g., Fig. 5).

Invasion by new plant species, one of the key threatening processes, was more prominent in wetland 2 than wetland 1. Even though we did not detect any major filtering effect associated with weed diversity on the current beta diversity of natural species, it is likely that continued proliferation of weeds will have an impact (Alpert et al. 2000) resulting in a loss of key values (Charles and Dukes 2007). Weed species and their role in ecological assembly have received considerable attention in the general literature (e.g., Booth and Swanton 2002, Ryan et al. 2010, Sheppard et al. 2010, Storkey et al. 2010). When either existing species or species newly introduced to the regional species pool are able to negotiate the various dispersal and environmental filters for the first time to arrive and establish themselves, they will often have a profound effect on system assembly, especially if they are transformer species (Richardson et al. 2000). This would constitute a general assembly rule where the associated underlying mechanisms may be quite extensive, complex, and even irreversible. The very presence of newly established weed species means that the system has already, to some extent, re-assembled.

We can conclude that the dispersal filters acting around wetland 1 are now operating differently to wetland 2, which presumably relates to the proximity of surrounding cleared agricultural land and the hydrology of their respective catchments (topography, soil type, etc.). Depending on the dispersal mechanisms, appropriate revegetation around wetland 2 to approximate the riparian buffer surrounding wetland 1 may be an important management action. Interestingly, managing water movement may be one way to minimize weed dispersal (some species may disperse via water flow), but may impinge upon the ecosystem service potential of wetland 2. Our approach provides a mechanism to identify and resolve value conflicts. Which values are more important? Will the loss of one value suitably compensate for the maintenance of another and so on? For the specific case of the elements investigated in this study, can we find a way to maintain ecosystem service values while halting weed invasion, which, if left unchecked, may eventually erode scientific/education and opportunity values?

Connectivity to the surrounding farmland may carry additional and perhaps interacting risks in addition to greater exposure to weeds. If the substrate in wetland 2, for example, is transitioning to sandier soil types, it is possible that the system will become less suitable for natural species that are adapted to heavier clays. We make note of this because the emergence of M. lateritia was significantly lower in the sandier soils of wetland 2 in the glasshouse experiment, highlighting the possibility of an additional filtering effect that relates to the soil types of the wetlands. Finally, our other result of zero M. lateritia seedlings emerging from soil collected from either wetland, despite the abundance of viable seed in the canopy and the suitability of our experimental conditions to facilitate germination of this species, must relate to: (1) the positioning of viable seeds within the soil profile (Brock 2011), (2) removal of seeds, possibly as a result of predation (e.g., Janzen 1971, Louda 1982), or (3) a rapid loss of seed viability after release from capsules. Any of these possibilities will be mechanisms that relate to an assembly rule and, given the importance of M. lateritia, warrant further research consideration.

The delivery of system benefit values by the wetlands will rely upon the continued presence of vegetation structure in the vegetation communities which is conditional, within the broader context of the other two key values, upon the
continued dominance of *M. lateritia* within the overstory canopy stratum. The soil EC tolerance of *M. lateritia* is currently not known and *Melaleuca* as a genera exhibit highly varied responses to salinity and waterlogging (Niknam and McComb 2000). For the case study, a key action for the management of the wetlands might, therefore, be to determine the salinity tolerance of *M. lateritia* as its ongoing persistence is important for the key values. The relative salinity tolerance of *M. lateritia* compared to the understory taxa could also reveal the likelihood of interspecific competition and survival during salt accumulation in the root zone, particularly in wetland 1.

Conclusions

We propose that a hierarchy of filtering processes has resulted in the two elements reassembling along different pathways. Even though the differences in species diversity may currently be marginal (in terms of value expectations), reassembly is an ongoing process, and without appropriate management (e.g., of weeds and hydrology) we can expect to see increasing differences between the two elements over time, with consequences for the values they are expected to deliver. However, with management, it may be possible to maintain the values currently associated with the system. Importantly, successful management will hinge on an understanding of the processes that control the assembly of biological elements, especially in relation to key threatening processes such as altered hydrology. This is important because the natural diversity of a biological element and the provision of structure have direct links to important human values for the case study area (Department of Parks and Wildlife 2013) and more broadly (e.g., the work of Shelby et al. 2005 relates to variation in vegetation structure). In our case study, we propose that vegetation diversity and structure must be maintained to ensure the associated values are retained. From this work, we suggest that management interventions should strive to (1) manage weeds, (2) control soil moisture content and soil EC, and (3) better understand within-wetland distribution of propagules—given the significant and different spatial patterning in the seed bank diversity of the two systems. Increased understanding of the tolerances of mature plants, seedlings, and propagules to salinity, waterlogging, and other potential threats is also critical to ensure management is informed and the contribution of the elements to human wellbeing are maintained.

Acknowledgments

We thank the Western Australian Department of Parks and Wildlife as part of the State Salinity Strategy and the Future Farm Industries Cooperative Research Centre for providing funding for the project. We thank Loretta Lewis for providing assistance in the field, Ray Froend and Gary Ogden for equipment loans, Bart Huntly for advice on spatial analysis, Mike Lyons for help with the plant identification, Andrew Crawford for advice and lab access to dehisce seeds and test germination, and Ken Wallace and Lindsay Bourke for their valuable comments on the manuscript.

Literature Cited

Alpert, P., E. Bone, and C. Holzapfel. 2000. Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. Perspectives in Plant Ecology Evolution and Systematics 3:52–66.

Arcioni, E. 2004. What’s in a name? The changing definition of weeds in Australia. Environmental and Planning Law Journal 2004:450–465.

Belyea, L. R., and J. Lancaster. 1999. Assembly rules within a contingent ecology. Oikos 86:402–416.

Blanchet, F. G., P. Legendre, and D. Borcard. 2008. Modelling directional spatial processes in ecological data. Ecological Modelling 215:325–336.

Booth, B. D., and C. J. Swanton. 2002. 50th anniversary: invited article. Assembly theory applied to weed communities. Weed Science 50:2–13.

Borcard, D., F. Gillet, and P. Legendre. 2011. Numerical ecology with R. Springer, New York, New York, USA.

Bouldina, J. L., J. L. Farrisa, M. T. Mooreb, and C. M. Cooperb. 2004. Vegetative and structural characteristics of agricultural drainages in the Mississippi Delta landscapes. Environmental Pollution 132:403–411.

Brauman, K. A., G. C. Daily, T. Ka’eo Duarte, and H. A. Mooney. 2007. The nature and value of ecosystem services: an overview highlighting hydrologic services. Annual Review of Environmental Resources 32:67–98.

Brock, M. A. 2011. Persistence of seed banks in Australian temporary wetlands. Freshwater Biology 56:1312–1327.

Brosi, B. J., M. J. Balick, R. Wolkow, R. Lee, M. Kostka, W. Raynor, R. Gallen, A. Raynor, P. Raynor, and
D. Lee Ling. 2007. Cultural erosion and biodiversity: canoe-making knowledge in Pohnpei, Micronesia. Conservation Biology 21:875–879.

Burgman, M. 2005. Risks and decisions for conservation and environmental management. Cambridge University Press, Cambridge, UK.

Capon, S. J., and M. A. Brock. 2006. Flooding, soil seed bank dynamics and vegetation resilience of a hydrologically variable desert floodplain. Freshwater Biology 51:206–223.

Carpenter, S. R. 2003. Regime shifts in lake ecosystems: pattern and variation. Excellence in Ecology Series 15. International Ecology Institute, Oldendorf/Luhe, Saxony, Germany.

Carter, J. L., T. D. Colmer, and E. J. Veneklaas. 2006. Variable tolerance of wetland tree species to combined salinity and waterlogging is related to regulation of ion uptake and production of organic solutes. New Phytologist 169:123–134.

Carter, J. D., and S. L. Lipple. 1982. Moora, Western Australia: sheet SH50/10 international index. Geological Survey of Western Australia, Perth, Western Australia, Australia.

Chang, C.-R., P.-F. Lee, M.-L. Bai, and T.-T. Lin. 2004. Predicting the geographical distribution of plant communities in complex terrain: a case study in Fushan Experimental Forest, northeastern Taiwan. Ecography 27:577–588.

Chapin, F. S., et al. 2000. Consequences of changing biodiversity. Nature 405:234.

Charles, H., and J. S. Dukes. 2007. Impacts of invasive species on ecosystem services. Pages 217–235 in M. M. Caldwell, G. Heldmaier, R. B. Jackson, O. L. Lange, H. A. Mooney, E.-D. Schulze, and U. Sommer, editors. Biological invasions. Springer-Verlag, Heidelberg, Germany.

Chow, W., R. Vogwill, and M. Forbes. 2010. Floristic values and hydrological threats to freshwater claypans in Drummond Nature Reserve, Western Australia. Australasian Plant Conservation 18:13–14.

Costanza, R., R. d’Arge, R. de Groot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R. V. O’Neill, J. Paruelo, R. G. Raskin, P. Sutton, and M. van den Belt. 1997. The value of the world’s ecosystem services and natural capital. Nature 387:253–260.

Crawley, M. J. 1996. The structure of plant communities. Pages 475–531 in M. J. Crawley, editor. Plant ecology. Blackwell, Oxford, UK.

Crist, T. O., J. A. Veech, J. C. Gering, and K. S. Summerville. 2003. Partitioning species diversity across landscapes and regions: a hierarchical analysis of a, b, and g diversity. American Naturalist 162:734–743.

Davis, J. A., and R. Froend. 1999. Loss and degradation of wetlands in southwestern Australia: underlying causes, consequences and solutions. Wetlands Ecology and Management 7:13–23.

Davis, J. A., M. McGuire, S. A. Halse, D. Hamilton, P. Horwitz, A. J. McComb, R. H. Froend, M. Lyons, and L. Sim. 2003. What happens when you add salt: predicting impacts of secondary salinisation on shallow aquatic ecosystems by using an alternative-states model. Australian Journal of Botany 51:715–724.

Department of Parks and Wildlife. 2013. Drummond Natural Diversity Recovery catchment recovery plan 2011–2031. Department of Parks and Wildlife, Perth, Western Australia, Australia.

Dray, S., P. Legendre, and P. R. Peres-Neto. 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecological Modelling 196:483–493.

Dudgeon, D., A. H. Arthington, M. O. Gessner, Z.-I. Kawabata, D. J. Knowler, C. Lévêque, R. J. Naiman, A.-H. Prieur-Richard, D. Soto, M. L. J. Stiassny, and C. A. Sullivan. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Reviews 81:163–182.

Forbes, M., and R. Vogwill. 2012. A geochemical investigation of hydrologically derived threats to rare biota: the Drummond Nature Reserve, Western Australia. Hydrogeology Journal 20:167–183.

Gadgil, M. 1992. Conserving biodiversity as if people matter: a case study from India. Ambio 21:266–270.

Garcia-Llorente, M., B. Martin-Lopez, S. Diaz, and C. Montes. 2011. Can ecosystem properties be fully transplanted into service values? An economic valuation of aquatic plant services. Ecological Applications 21:3083–3103.

George, P. R., and B. A. Wren. 1985. Crop tolerance to salinity. Technote number 6/85. Western Australian Department of Agriculture, Perth, Western Australia, Australia.

Gianaucia, A. T., V. A. G. Bastazini, R. A. Dias, and M. I. M. Hernández. 2013. Independent and shared effects of environmental features and space driving avian community beta diversity across a coastal gradient in southern Brazil. Austral Ecology 38:864–873.

Götzenberger, L. et al. 2012. Ecological assembly rules in plant communities—approaches, patterns and prospects. Biological Reviews 87:111–127.

Hart, B. T., P. Bailey, R. Edwards, K. Horte, K. James, A. McMahon, C. Meredith, and K. Swadling. 1991. A review of salt sensitivity of the Australian freshwater biota. Hydrobiologia 210:105–144.

Hobbs, R. J., and D. A. Norton. 2004. Ecological filters, thresholds and gradients in resistance to ecosystem reassembly. Pages 85–103 in V. M. Temperton, R. J. Hobbs, T. Nuttle, and S. Halle, editors. Assembly rules and restoration ecology. Island Press, Washington, D.C., USA.
James, K. R., B. Cant, and T. Ryan. 2003. Responses of freshwater biota to rising salinity levels and implications for saline water management: a review. Australian Journal of Botany 51:703–713.

Janzen, D. H. 1971. Seed predation by animals. Annual Review of Ecology and Systematics 2:465–492.

Keene, R. L. 1992. Value-focused thinking: a pathway to creative decision making. Harvard University Press, Cambridge, Massachusetts, USA.

Keighery, G. J., N. Gibson, A. Webb, and W. P. Muir. 2002. A biological survey of the agricultural zone: vegetation and vascular flora of Drummond Nature Reserve. Conservation Science Western Australia 4:63–78.

Ladiges, P. Y., P. C. Foord, and R. J. Willis. 1981. Salinity and waterlogging tolerance of some populations of Melaleuca ericifolia Smith. Australian Journal of Ecology 6:203–215.

Leck, M. A. 1989. Wetland seed banks. Pages 283–305 in M. A. Leck, V. T. Parker, and R. L. Simpson, editors. Ecology of soil seed banks. Academic Press, New York, New York, USA.

Leck, M. A., and R. L. Simpson. 1987. Seed bank of a freshwater tidal wetland: turnover and relationship to vegetation change. American Journal of Botany 74:360–370.

Legendre, P., D. Borcard, and P. R. Peres-Neto. 2005. Analyzing beta diversity: partitioning the spatial variation of community composition data. Ecological Monographs 75:435–450.

Lindemann-Matthies, P., X. Junge, and D. Matthies. 2010. The influence of plant diversity on people's perception and aesthetic appreciation of grassland vegetation. Biological Conservation 143:195–202.

Louda, S. M. 1982. Distribution ecology: variation in plant recruitment over a gradient in relation to insect seed predation. Ecological Monographs 52:25–41.

Lyons, M. N., N. Gibson, G. J. Keighery, and S. D. Lyons. 2004. Wetland flora and vegetation of the Western Australian wheatbelt. Records of the Western Australian Museum Supplement 67:39–89.

Macfarlane, C., and G. N. Ogden. 2012. Automated estimation of foliage cover in forest understory from digital nadir images. Methods in Ecology and Evolution 3:405–415.

McDonald, R. C., R. F. Isbell, J. G. Speight, J. Walker, and M. S. Hopkins. 1990. Australian soil and land survey: field handbook. Second edition. Inkata Press, Melbourne, Victoria, Australia.

Metcalf, S. J., and K. Wallace. 2013. Ranking biodiversity risk factors using expert groups: treating linguistic uncertainty and documenting epistemic uncertainty. Biological Conservation 162:1–8.

Millennium Ecosystem Assessment. 2005. Ecosystems and human well-being: synthesis. Island Press, Washington, D.C., USA.

Mitsch, W. J., and J. G. Gosselink. 2007. Wetlands. John Wiley and Sons, New York, New York, USA.

Morris, K., P. C. Bailey, P. I. Boon, and L. Hughes. 2003. Alternative stable states in the aquatic vegetation of shallow urban lakes. II. Catastrophic loss of aquatic plants consequent to nutrient enrichment. Marine and Freshwater Research 54:201–215.

Munns, R. 2002. Comparative physiology of salt and water stress. Plant, Cell and Environment 25:239–250.

Munns, R., and A. Termaat. 1986. Whole-plant responses to salinity. Australian Journal of Plant Physiology 13:143–160.

Nielsen, D. L., M. A. Brock, G. N. Rees, and D. S. Baldwin. 2003. Effects of increasing salinity on freshwater ecosystems in Australia. Australian Journal of Botany 51:655–665.

Niknam, S. R., and J. McComb. 2000. Salt tolerance screening of selected Australian woody species: a review. Forest Ecology and Management 139:1–19.

Peres-Neto, P. R., P. Legendre, S. Dray, and D. Borcard. 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. Ecology 87:2614–2625.

Poschlod, P., M. Abedi, M. Bartelheimer, J. Drobnik, S. Rosbakh, and A. Saatkamp. 2012. Seed ecology and assembly rules in plant communities. Pages 164–202 in E. van der Maarel and J. Franklin, editors. Vegetation ecology. John Wiley and Sons, Chichester, West Sussex, UK.

Pouwels, R., P. Opdam, and R. Jochem. 2011. Reconsidering the effectiveness of scientific tools for negotiating local solutions to conflicts between recreation and conservation with stakeholders. Ecology and Society 16:17.

Primack, R. B., and S. L. Miao. 1992. Dispersal can limit local plant distribution. Conservation Biology 6:513–519.

Quirk, J. P., C. Pereira, and T. W. Tanton. 1986. Soil permeability in relation to sodicity and salinity. Philosophical Transactions of the Royal Society A: Mathematical and Physical Sciences 316:297–317.

R Development Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ribe, R. G. 2005. Aesthetic perceptions of green-tree retention harvests in vista views. The interaction of cut level, retention pattern and harvest shape. Landscape and Urban Planning 73:277–293.

Richardson, D. M., P. Pysek, M. Rejmanek, M. G. Barbour, F. D. Panetta, and C. J. West. 2000. Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions 6:93–107.

Ryan, M. R., R. G. Smith, S. B. Mirsky, D. A. Mortensen, and R. Seidel. 2010. Management filters and species traits: weed community assembly in
Salter, J., K. Morris, and P. I. Boon. 2008. Does salinity reduce the tolerance of two contrasting wetland plants, the submerged monocot Vallisneria australis and the woody shrub Melaleuca ericifolia, to wetting and drying? Marine and Freshwater Research 59:291–303.

Sax, D. F., and S. D. Gaines. 2003. Species diversity: from global decreases to local increases. Trends in Ecology and Evolution 18:561–566.

Scheffer, M., and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. Trends in Ecology and Evolution 18:648–656.

Scheffer, M., S. R. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature 413:591–596.

Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012. NIH Image to Image J: 25 years of image analysis. Nature Methods 9:671–675.

Shainberg, I., and J. Letey. 1984. Response of soils to sodic and saline conditions. Hilgardia 52:1–57.

Shelby, B., J. R. Thompson, M. Brunson, and R. Johnson. 2005. A decade of recreation ratings for six silviculture treatments in Western Oregon. Journal of Environmental Management 75:239–246.

Smith, M. J., K. M. Ough, M. P. Scroggie, E. S. G. Schreiber, and M. Kohout. 2009. Assessing changes in macrophyte assemblages with salinity in non-riverine wetlands: a Bayesian approach. Aquatic Botany 90:137–142.

Storkey, J., S. R. Moss, and J. W. Cussans. 2010. Using assembly theory to explain changes in a weed flora in response to agricultural intensification. Weed Science 58:39–46.

Turner, R. K., C. J. M. van den Bergh, T. Söderqvist, A. Barendregt, J. van der Straaten, E. Maltby, and E. C. van Ierland. 2000. The values of wetlands: landscape and institutional perspectives. Ecological Economics 35:7–23.

United Nations. 1992. Convention on biological diversity. United Nations, Geneva, Switzerland.

Vengosh, A. 2014. Salinization and saline environments. Pages 325–378 in H. D. Holland and K. K. Turekian, editors. Treatise on geochemistry. Second edition. Elsevier, Oxford, UK.

Wallace, K. 2012. Values: drivers for planning biodiversity management. Journal of Environmental Policy and Planning 17:1–11.

Wallace, K. J., B. C. Beecham, and B. H. Bone. 2003. Managing natural biodiversity in the Western Australian wheatbelt: a conceptual framework. Department of Conservation and Land Management, Perth, Western Australia, Australia.

Walshe, T. 2005. Decision framework for Natural Diversity Program: scoping project. Department of Conservation and Land Management, Perth, Western Australia, Australia.

Walshe, T., S. Jones, and T. Massenbauer. 2007. Decision framework for Natural Diversity Recovery Program (implementation). University of Melbourne, Melbourne, Victoria, Australia.
### APPENDIX A

**Species lists and codes**

Table A1. Wetland 1 natural species list and codes used for graphing.

| Identity                  | Graphing code |
|---------------------------|---------------|
| Gonocarpus/Haloragis sp.  | GoHa          |
| Apium annuum†             | Aann          |
| Blennospora drummondii     | Bdru          |
| Calandrinia sp. (GK id) 1 | Casp1         |
| Centroplepis aristata     | Cari          |
| Centroplepis glabra       | Cgla          |
| Centroplepis pilosa†      | Cpil          |
| Centroplepis sp. 1        | Csp1          |
| Centroplepis sp. 2        | Csp2          |
| Gratiola pubescens†       | Gpub          |
| Hydrocotyle lemnoides     | Hlem          |
| Hydrocotyle sp. 1         | Hsp1          |
| Hydrocotyle sp. 2         | Hsp2          |
| Indet sp. 1 (sterile herb)| Ind1          |
| Myriophyllum drummondii†  | Mdru          |
| Schoenus tenellus         | Ste1          |
| Sterile sp. 1             | Unk1          |
| Sterile sp. 2             | Unk2          |
| Stylidium despectum†      | Tbib          |
| Unknown sp. 1             | Unk3          |
| Unknown sp. 2             | Unk4          |
| Unknown sp. 3             | Unk5          |

† Species found in this study but not in the survey of Keighery et al. (2002).

Table A2. Wetland 2 natural species list and codes used for graphing.

| Identity                  | Graphing code |
|---------------------------|---------------|
| Apium annuum†             | Aann          |
| Blennospora drummondii     | Bdru          |
| Calandrinia sp. (GK id) 1 | Casp1         |
| Centroplepis aristata     | Cari          |
| Centroplepis sp. 1        | Csp1          |
| Crassula exserta          | Cexs          |
| Gnephosis tenuissima†     | Gten          |
| Gratiola pubescens†       | Gpub          |
| Hydrocotyle lemnoides     | Hlem          |
| Hydrocotyle sp. 1         | Hsp3          |
| Indet sp. 2               | Ind2          |
| Myriophyllum drummondii†  | Mdru          |
| Schoenus odontocarpus†    | Sodo          |
| Schoenus tenellus         | Ste1          |
| Schoenus? loliaceus GJK 15488 | Stol       |
| Sterile sp. 1             | Ste1          |
| Stylidium despectum†      | Sdes          |
| Unknown sp. 1             | Unk3          |
| Unknown sp. 2             | Unk4          |
| Unknown sp. 3             | Unk5          |

† Species found in this study but not in the survey of Keighery et al. (2002).

Table A3. Introduced species list and codes used for graphing.

| Identity                  | Graphing code | Wetland |
|---------------------------|---------------|---------|
| Crassula natans†          | Cnat          | 1 and 2 |
| Hordeum vulgare†          | Hvul          | 2       |
| Vulpia myuros†            | Vmyu          | 2       |
| Cicendia filiformis       | Cfil          | 2       |
| Juncus biflorus†          | Jbuf          | 2       |

† Species found in this study but not in the survey of Keighery et al. (2002).

†† Species detected by Keighery et al. (2002), but not in the claypans.
APPENDIX B

Forward selected spatial descriptors

Fig. B1. Forward selected spatial descriptors (PCNM variables) for wetland 1 study sites. Black symbols are positive and white symbols negative. Size of symbol increases with the magnitude of the site score.

Fig. B2. Forward selected spatial descriptors (PCNM variables) for wetland 2 study sites. Black symbols are positive and white symbols negative. Size of symbol increases with the magnitude of the site score.