CrossMark

ORIGINAL PAPER

Diversity patterns of seasonal wetland plant communities mainly driven by rare terrestrial species

David C. Deane[1,2] · Damien A. Fordham[1] · Fangliang He[2,3] ·
Corey J. A. Bradshaw[1]

Abstract In cleared landscapes, wetlands can represent important reservoirs of native plant diversity, which include terrestrial species. Depending on study aims, non-wetland plants might be removed before analysis, affecting conclusions around biodiversity and community structure. We compared the native plant communities of seasonal wetlands in a predominately agricultural landscape as defined geographically (including all species) with that of the obligate wetland assemblage. We were primarily concerned with determining how this design decision affects ecological and conservation conclusions. We analysed a survey database containing >12,900 flora records from South Australia, developing a new area-based method to remove sampling bias to include only wetlands with a near-complete census. We modelled occupancy, species-area relationships, β-diversity and nestedness under our contrasting community definitions. Terrestrial species were 57.4 % of total richness. Removing these species reduced wetland α-diversity by 45 %, but did not affect the scaling of richness with area (power-law species-area relationship $z = 0.21 \pm 0.01$). Occupancies for wetland plants were relatively uniform, but were heavily dominated by rare (satellite) species when terrestrial plants were included, and this also increased β-diversity. Nestedness for terrestrial species occupancies was marginally lower than predicted under null models, suggesting that rare species often do not co-occur with common species. An implication of these occupancy patterns is that twice as many wetlands (and

✉ David C. Deane
   david.deane@adelaide.edu.au

1   School of Biological Sciences, University of Adelaide, Adelaide, SA 5005, Australia

2   SYSU—Alberta Joint Lab for Biodiversity Conservation, State Key Laboratory of Biocontrol and School of Life Sciences, Sun Yat-sen University, Guangzhou 510275, People's Republic of China

3   Department of Renewable Resources, University of Alberta, Edmonton, AB T6G 2H1, Canada

50 % more wetland area) would be needed to include every native species within at least one wetland compared with *wetland-only* species.

Introduction

Wetlands, like all freshwater ecosystems, are susceptible to many stressors arising from global change (Davis et al. 2010; Dudgeon 2010; Houlahan et al. 2006). Seasonal wetlands are among the most vulnerable to human activities (Holland et al. 1995), but they also support species-rich ecotones (Brock and Casanova 1997) that provide habitat for both wetland and terrestrial (often called 'upland') plant species (Brose 2001; Haukos and Smith 1994; Kaeser and Kirkman 2009). Even in highly urbanised or agricultural catchments, at least some wetland or riparian areas remain and these can represent the only remaining areas of native vegetation (Haukos and Smith 1994; Lastrucci et al. 2010; von Behren et al. 2013).

Studies of wetland plant biodiversity can, depending on the research aims, choose to limit analyses to obligate wetland species—a question of community definition (Fauth et al. 1996). If research interest is on biodiversity of all plants occurring within the mapped wetland extent, then a geographical definition of 'community' applies (and terrestrial species should be retained); alternatively, interest could lie only in obligate wetland plants and this assemblage would then define the community (Fauth et al. 1996). From a regional biodiversity perspective, particularly in cleared landscapes where little other native vegetation remains, the decision of whether or not to omit terrestrial species from wetland datasets is important because it risks developing an incomplete understanding of the full suite of species that depend on the presence of those habitat patches. It could also change conclusions about community-assembly processes with implications for conservation planning. We therefore compared the results of omitting or including terrestrial species when evaluating the biodiversity patterns of seasonal wetland plant communities in heavily cleared agricultural landscapes in South Australia. Study wetlands are of high conservation value both as habitat for endangered fauna (Wilson and Paton 2004) and for their intrinsic values (Duffield et al. 2000), and are classified as a Critically Endangered community under the federal *Environment Protection and Biodiversity Conservation Act 1999*. We expected to find that terrestrial species are also an important component of these seasonal wetland plant communities, contributing to regional biodiversity conservation.

Effective conservation planning requires an understanding of species abundances, spatial distributions of species and richness patterns, in particular diversity and endemicity (Rodrigues and Gaston 2001). However, obtaining sufficient data to do this can be challenging. Fortunately, museum or herbaria databases (Delgado et al. 2005) and other 'natural history collections' (Graham et al. 2004) can provide occurrence data useful for correlative and mechanistic species distribution modelling (Elith et al. 2006; Fordham et al. 2012). Other online databases also provide survey data collated over

many projects, which have potential uses in other forms of modelling. While Balian et al. (2008) have called for the increased use of these survey databases for applications in freshwater biodiversity, there are technical challenges in their use that are often overlooked (e.g. Hortal et al. 2007; Soberon and Peterson 2004). It remains unclear to what extent these databases can contribute to modelling wetland biodiversity patterns or species extinction risk.

We tested whether an existing plant survey database could be used for modelling patterns of biodiversity in wetland plant communities, testing hypotheses on how the inclusion or exclusion of terrestrial species affect conclusions. We expected decreased compositional similarity (higher β-diversity) when including terrestrial plants due to the much larger species-pool for terrestrial—(compared with obligate-wetland) plants (Chambers et al. 2008). For similar reasons we expected that excluding terrestrial species would increase nestedness in plant communities (species-poor sites would be proper subsets of species-rich sites). Finally, because including terrestrial species must increase wetland α-diversity, we expected to find higher intercepts and changes to the slopes of species-area relationships (Brose 2001; Smith and Haukos 2002). We show that the terrestrial component of these seasonal wetlands is not only diverse and highly variable, but that the distribution of rare terrestrial species (those found in <10 % of wetlands) does not necessarily coincide with that of common species. This finding greatly increases both the number and total area that is required to protect the regional plant biodiversity as determined by seasonal wetlands in this heavily modified landscape.

Table 1 Regional database and analysis dataset summary statistics

Region	Rainfall range	500–800 mm/year
	Maximum elevation	320 m
	Central latitude	35.5°S
Analysis dataset	Total wetlands	76
	Median size	2.8 ha
	Mean size	4.5 ha
	Maximum size	34.7 ha
	Mean richness (all native plants) [95 % CI]	30 [28.1, 32.6]
	Mean richness (*wetland-only* natives) [95 % CI]	21 [18.9, 21.9]
	Mean richness (*terrestrial* natives) [95 % CI]	10 [9.2, 11.5]
	β_1 *all native plants*	0.09
	β1 wetland-only natives	0.06
	β_1 *terrestrial natives*	0.17
	Native *terrestrial* species	124
	Exotic *terrestrial* species	100 (32 %)
	Terrestrial rare or endangered species	10 (8 %)
	Native *wetland-only* species	91
	Exotic *wetland-only* species	18 (16 %)
	Wetland rare or endangered species	16 (18 %)

Methods

Study area

We collated data specific to wetlands located on the Fleurieu Peninsula in South Australia covering an area of 1200 km^2 (Clark et al. 2007) and extending 100 km to the south west of Adelaide (Table 1; Fig. 1). The region's climate is Mediterranean, with warm, dry summers and cool, wet winters. Average annual rainfall at sea level is 500 mm and this increases to around 900 mm in the highest-elevation ($\sim$320 m) central plateaux. The wetlands comprise dense vegetation that is described as 'reedy or heathy' and growing on waterlogged soils typically associated with watercourses (Duffield et al. 2000). Inundation of wetland substrata is generally shallow and seasonal, although permanent areas of surface saturation associated with springs are common. Areas of open water are rare and tend to be within the shallow watercourses typical of core wetland areas. As a result, while terrestrial species are more abundant in fringing locations, they can often be found in drier micro-sites throughout the wetland extent.
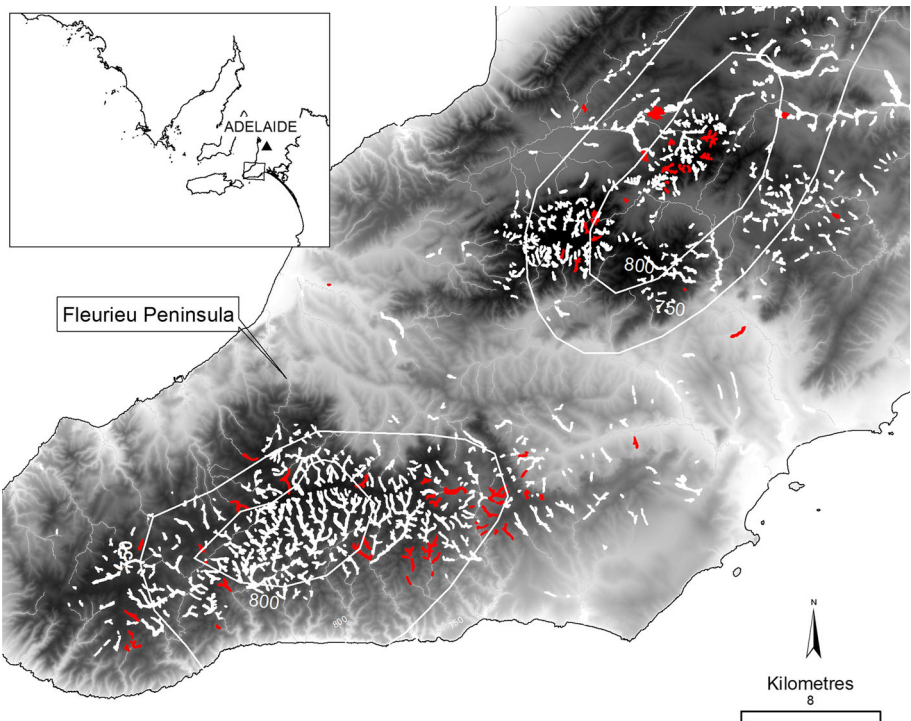
Fig. 1 Fleurieu Peninsula, South Australia showing study wetlands in red and other wetlands in white. Also shown are 750 and 800 mm isohyets and major watercourses. Shading represents topography, with dark shades indicating higher elevations that reach a maximum of $\sim$320 m above sea level. Fleurieu wetlands occur mostly above elevations of around 250 m coinciding with mean annual rainfall >750 mm

Data

We started with a published survey database (South Australian Wetland Inventory Data-base—SAWID) compiled during a wetland mapping and data inventory project on the Fleurieu Peninsula, South Australia (Harding 2005). We defined our wetland areas according to the mapping data from that project, which applied a consistent protocol described in Harding (2005). All available biological data collected from 1977 to 2004 were incorporated within the database, which included a range of data types collected across more than 20 projects. We updated this database with three additional wetland vegetation surveys done from 2005 to 2009. Survey methods included opportunistic sightings (herbaria data), species lists, and quadrat-based surveys. We matched all flora records to the relevant alphanumeric taxonomic codes used in the Biological Database of South Australia (BDBSA; www.environment.sa.gov.au/Science/Information_data/ Biological_databases_of_South_Australia) to ensure consistency across datasets. We also used the BDBSA to determine conservation status and exotic plants, removing all non-native plants from further analysis (note that exotic plants do not affect overall conclusions—Appendix 6, Supporting Information).

Data pre-processing and removal of sampling bias

To ensure ecologically meaningful comparisons, we separated flora records by decade and used data from only the most recent decade (2000–2009), during which time no widespread changes in land use have occurred. Records collected prior to 2000 represented only around 25 % of records and were insufficient to support any comparison with wetlands during the most recent decade.

Following the general methods described in Hortal et al. (2007), we first did a range of quality checks on records, removing, or where possible, correcting spatial information based on comparison of the recorded coordinates of surveys, metadata describing the actual location and wetland extent mapping. Species richness was positively correlated with survey effort (measured as number of surveys), which is an indication of sampling bias that had to be removed prior to analysis. We first attempted to use published methods to do this (e.g., Hortal et al. 2007; Lobo 2008), but were unsuccessful (discussed in Appendix 1). We instead used a three-step process to select wetlands with near-complete surveys: (i) we fitted a power-law species-area relationship using wetlands known to have a good census record, (ii) we calculated a prediction interval based on the observed species-area relationship, and (iii) we applied this prediction interval criterion on all wetlands in the database, selecting those where observed species richness fell within the prediction interval for a wetland of that size. Below we discuss each step individually.

Fitted species-area relationship

We started with two subsets of the data: a *baseline* dataset only including wetlands known to have a reliable census record (surveyed or co-surveyed by D.C.D, $n = 11$); an *incomplete* dataset containing only surveys we considered very unlikely to be full-census records based on their spatial design and scaling with area ($n = 14$; see Appendix 1). *Baseline* wetlands were located from across the region and covered a wide range in total area (0.5–34.5 ha). They also included example wetlands from catchments under all of the dominant land uses in the region (grazing, plantation forestry and both private and formal

conservation). We fitted a power-function species-area relationship to the *baseline* dataset ($S = cA^z$ where: S = species richness, A is wetland area, while c and z are constants; Fig. 2). Model parameter values ($c = 29.3$ [24.7, 34.0] (mean ± [95 % confidence intervals]); $z = 0.25$ [0.185, 0.322]) were in the range of values typical for similar wetlands (Tables A-2, A-3) and area explained a high proportion of variation in species richness ($R^2 = 0.88$; Fig. 2a). We therefore assumed that variation in the species-area relationship for *baseline* wetlands was typical of the range for all wetlands in the region.

Selecting prediction intervals

We then calculated prediction intervals for the species-area model that included the maximum number of *baseline* wetlands, while precluding all *incomplete* wetlands. We calculated prediction intervals using the delta method to estimate the variance of the power-function:

$$y \pm \sqrt{G'\left(\hat{\beta}, x\right)^T Var\left(\hat{\beta}\right) G'\left(\hat{\beta}, x\right)} \times \hat{\sigma}^2 \times t_{\alpha/2, n-2} \tag{1}$$

where: y is the estimated species richness at area x; $G'\left(\hat{\beta}, x\right)$ and $G'\left(\hat{\beta}, x\right)^T$ are the derivative of the power-function with respect to the parameter vector β evaluated at value x using the best fit estimates, and its transpose respectively; $Var\left(\hat{\beta}\right)$ is the variance–covariance matrix for the model parameters; $\hat{\sigma}^2$ is the estimated error variance (the square-root of the sum of the squared errors divided by the model degrees of freedom); and, $t_{\alpha/2, n-2}$ is the critical value for the *t*-distribution at confidence level $(1-\alpha)$.
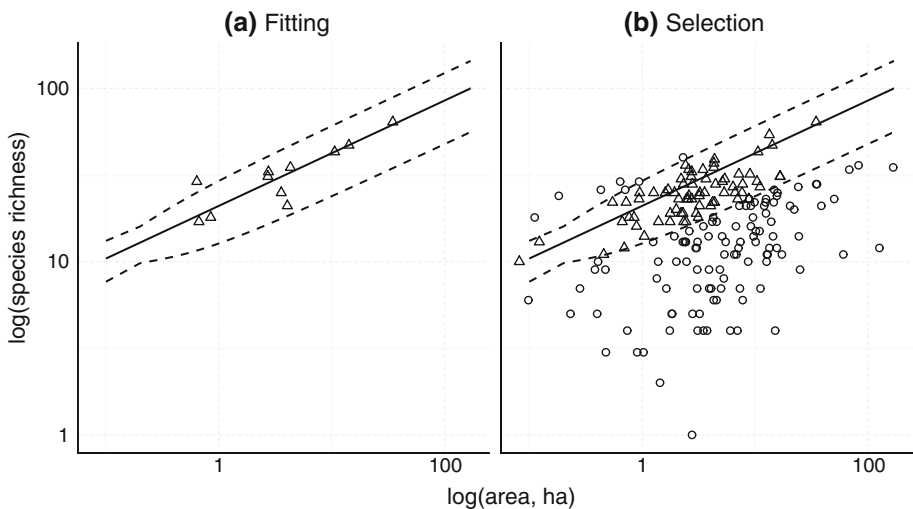
Fig. 2 Power-law species-area relationships fitted to (**a**) baseline wetlands and (**b**) used to select full-census wetland surveys (logarithmic-scaling of axes). In both panels, the *solid line* is the best-fit power-law species-area curve and *dashed lines* are 50 % prediction intervals for the model. In panel (**b**), wetlands included in the analysis set are symbolised by *triangles*, and omitted wetlands by *circles*

We selected the value of α where prediction intervals for the species-area relationship included the maximum number of *baseline* wetlands but did not select any from the *incomplete* wetlands. These criteria suggested a 50 % prediction interval. Although this excluded one of the *baseline* wetlands (Fig. 2a), a prediction interval wide enough to include this wetland included almost every wetland in the dataset.

Wetland selection using prediction intervals

Using Eq. 1 and α = 0.5 we calculated a 50 % prediction interval for species richness for all mapped wetlands with flora data collected after 1999 ($n = 185$). We selected all wetlands where the observed species richness fell within this prediction interval (Fig. 2b). A total of 80 wetlands met this criteria. We removed four wetlands with areas less than 0.4 ha to avoid extrapolating too far below our minimum observed wetland area (0.54 ha). Our final analysis dataset consisted of 76 wetlands.

We recognise that precluding wetlands falling above the prediction interval could result in the loss of legitimate surveys from wetlands of unusually high diversity. Equally, in addition to the desired effect of filtering out incompletely surveyed wetlands, our approach could remove wetlands of unusually low diversity. We saw no alternative to the use of area-scaling relationships as size differences among wetlands make it impossible to use established methods as discussed above (e.g., Hortal et al. 2007; Lobo 2008). Given the strength of the species-area relationship in our *baseline* dataset, and the consistency of parameter estimates in our predictive model with published values, we believe that our analysis dataset provides a reliable statistical sample of these wetland plant communities.

Separating obligate- and non-obligate wetland plant species

We used the water plant functional group assignments of Casanova and Brock (2000) to distinguish obligate wetland plants from those capable of persisting within the terrestrial landscape matrix. We based our assignment into functional groups on Casanova (2011) and the opinion of local aquatic botanists (*pers. comm.* J. Nicol, South Australian Research and Development Institute). We omitted from the *wetland-only* subset plants classified as terrestrial, which are represented by functional groups 'Tdry' and 'Tdamp' (Casanova 2011). This is similar to excluding both facultative and obligate upland plants from the wetland community if using the US Department of Interior wetland plant classification (Reed 1988). Our final two wetland-community datasets comprised *all plants* and *wetland-only* taxonomic subsets of the native vegetation. We also analysed terrestrial species separately in some analyses to highlight differences between the obligate and non-obligate communities. We refer to this dataset as *terrestrial*, although strictly speaking it includes some facultative wetland plants.

Analysis

We analysed three major ecological patterns in each dataset: (i) species occupancy, (ii) species-area relationships, and (iii) distance-decay in community similarity—a form of species turnover or β-diversity (Anderson et al. 2011). To distinguish competing occupancy frequency distributions, we fitted seven regression models for ranked species occupancy curves (RSOC; Jenkins 2011). Six of these (concave and convex exponential; symmetric and asymmetric sigmoidal; lognormal and linear) were recommended in

Jenkins (2011) and the seventh (power exponential function) was suggested by Hui (2012). Models were selected using Akaike's information criterion (Burnham and Anderson 2002).

Although many different models have been proposed for species-area relationships [reviewed in Tjørve (2003)], the power function (Arrhenius 1921) has the most support in comparative studies (Drakare et al. 2006; Triantis et al. 2012). It was also the most widely applied species-area model, used in 22 of 28 studies done in lake and wetland ecosystems that we reviewed (Table A-2, Appendix 2). We fitted power-function species-area models to each dataset to test whether the value of the z parameter (slope) and coefficient of determination (R^2) differed between *wetland-only* and *all plants* communities.

β-diversity (Whittaker 1960) describes changes in community composition, or differentiation, and has been described using many different measures. To compare this value for our study with previously published wetland data, we used the 'beta-1' index of Harrison et al. (1992), which modifies Whittaker's (1960) multiplicative relationship: $\beta_1 = [\gamma/\bar{\alpha} - 1]/(N - 1)$, where γ = total observed species richness, α = mean wetland species richness, N = the number of wetlands, and β_1 can be interpreted as the average compositional turnover between wetlands (range 0–1) (Harrison et al. 1992). We selected this index because its simple data requirements allowed us to calculate the distribution of the statistic from published studies in shallow wetland systems for comparison (Table A-4, Appendix 3).

Distance-decay of similarity is also a measure of β-diversity, but is instead concerned with differentiation in species composition along a gradient (Nekola and White 1999). Modelling this relationship allows for the comparison of different samples (Anderson et al. 2011; Soininen et al. 2007), here represented by our two wetland plant communities. We used the complement of the pairwise Jaccard dissimilarity index as a measure of wetland community similarity and the Euclidean distance between wetland centroids to represent the geographical distance. Nekola and White (1999) suggested the negative exponential model to describe plant community distance-decay: $S = S_0 e^{-cd}$, where S = similarity at distance d, S_0 = the maximum similarity between two sites, and c is a fitting parameter. Linear, log–log and log-linear models are also commonly applied functions (Soininen et al. 2007). However, the distribution of the data suggested a functional form with a more rapid initial decay. We therefore fit a power function: $S = ad^{-b}$, where S and d take their above values, and a and b are fitted model parameters. We compared model support for the power, negative exponential, log–log and log-linear distance-decay functions using Akaike's information criterion. We compared the parameter values for the top-ranked model for both communities. We expected higher between-wetland similarity and that this should decay more slowly in *wetland-only* communities because of the smaller species pool for wetland plants and increased dispersal via waterways. We did all modelling using the R platform (R Core Team 2014) with custom analysis packages `betapart` (Baselga et al. 2013), `vegan` (Oksanen et al. 2013), `minpack.lm` (Elzhov et al. 2015) and data manipulation and plotting packages `reshape2` and `ggplot2` (Wickham 2007, 2009).
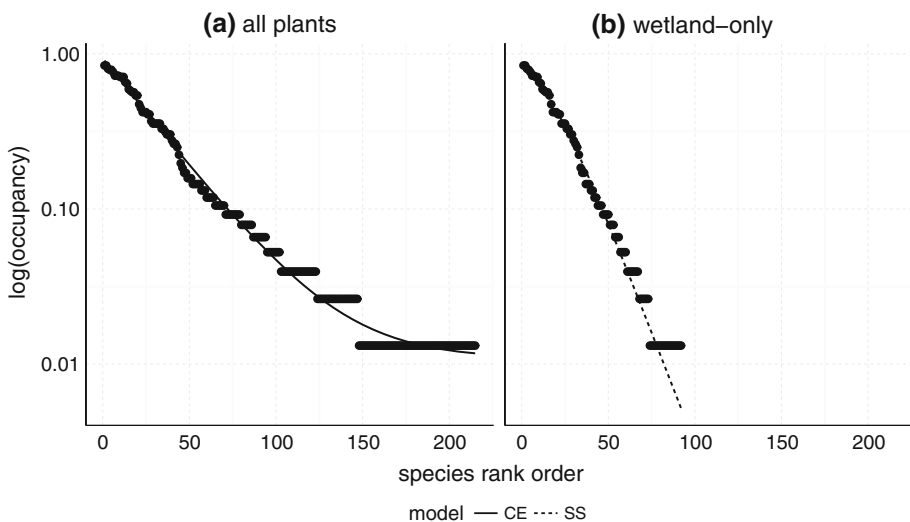
Ranked species occupancy curves are based on marginal totals and provide only limited insights of community patterns; we therefore also calculated nestedness within the two communities (Hui 2012). We predicted that *wetland-only* communities would be more nested than *all plants* due to the smaller regional species pool and the filtering effects of hydrological niche breadth. We used the nestedness metric based on overlap and decreasing fill from Almeida-Neto et al. (2008). This method determines the degree of nestedness for the overall matrix, but also the separate contributions of occupancy (nesting of species) and composition (nesting of sites). The metric ranges from 0 to 100, the upper extreme representing perfect nestedness. We did the nestedness analysis using the *NODF*

software package (Almeida-Neto and Ulrich 2011), which calculates the metric and provides a test of the null hypothesis that the observed overlap and decreasing fill metrics do not differ from expected values under the assumption of null communities. Simulated null communities are used to determine the expectation, using the proportional—algorithm (Ulrich and Gotelli 2012). A one-sided Type I error p is calculated for the Z-transform under an assumption of normally distributed values for the null communities overlap and decreasing fill metrics (calculated as $Z = [x - \mu]/\sigma$ where: x = the overlap and decreasing fill metric, μ and σ = mean and standard deviation, respectively for the distribution of the equivalent overlap and decreasing fill metric from 999 simulated communities).

Results

The number of surveys per wetland (range 1–10; median = 1) was positively correlated with species richness (Spearman rank correlation $\rho_s = 0.41$, $n = 219$, $p < 0.001$). Our sampling-bias-removal method identified 76 wetlands with a near-complete census. This represents 9 % of the total number of mapped wetlands and 41 % of the wetlands within the database with post-1999 flora records. Native species richness for the *all plants* and *wetland-only* analysis datasets were 215 and 91, respectively (Table 1). Proportionally, there were twice as many terrestrial species that were classed as 'exotic' compared to wetland species (32 vs. 16 %), and 18 % of *wetland-only* species were rare or endangered compared with 8 % of terrestrial species (Table 1). At the wetland scale, including terrestrial native plants increased mean species richness from (mean [± 95 % confidence limits] = 21 [18.9, 21.9]) to 30 [28.1, 32.6] (Table 1). Compared with the full wetland size distribution (Table A-1), the median size of full-census wetlands was larger (2.8 vs. 2.1 ha), but mean size was smaller (4.5 vs. 5.1 ha).

Fig. 3 Ranked species-occupancy curves for *all plants* (**a**) and *wetland-only* (**b**) datasets. The *x*-axis shows the rank order of each species (highest occupancy is ranked 1st). The top-ranked model is also shown, along with the coefficient of determination for each fit. *CE* concave exponential function, *SS* symmetric sigmoidal [see Jenkins (2011)]

Ecological patterns

Ranked species-occupancy curves for the two communities differed in shape, mostly due to more infrequently occurring terrestrial species when *all plants* were included (Fig. 3, Fig. A-4, Appendix 1). There was a corresponding difference in the top-ranked regression model: for *all plants* this was the concave exponential function; for *wetland-only* plants the symmetric sigmoidal function (Fig. 3; Table 2, Table A-7, Appendix 5). The AIC weight (*w*AIC ≈ parameter-corrected relative model probability) exceeded 0.99 for both models. The coefficient of determination for regression model fits were both >0.99 (Fig. 3). The occupancy frequency distribution for *all plants* was strongly unimodal and dominated by infrequently observed (satellite) species (Fig. A-4, Appendix 4) for *all plants*, but this mode was reduced for *wetland-only* plants, with a relative increase in frequently observed (core) species, particularly when compared with *terrestrial* species (Fig. A-5, Appendix 4).
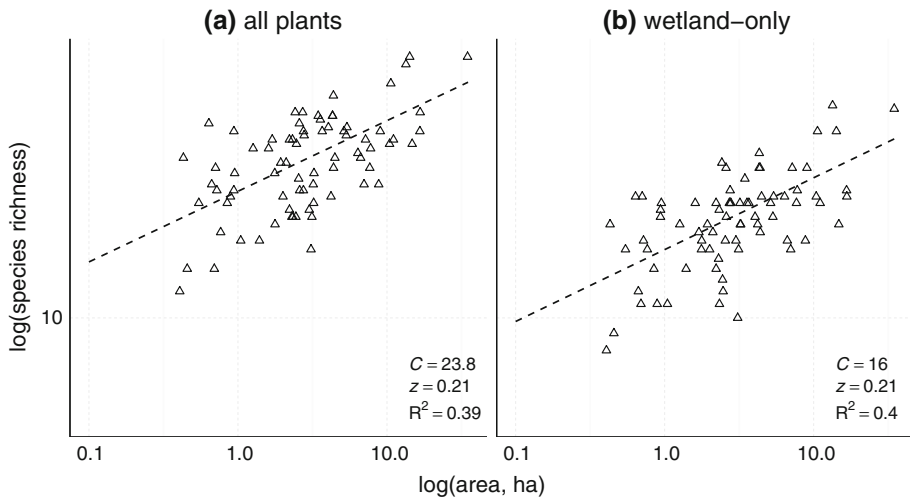
The power function species-area relationship had similar support for both the *all plants* and *wetland-only* datasets, the fit being marginally better when terrestrial plants were excluded ($R^2 = 0.39$ vs. 0.40; Fig. 4; Table 2). Slopes (z) were the same for the two

Table 2 Model coefficients and goodness of fit for three ecological patterns for *all plants* and the subsets *wetland-only* and *terrestrial* analysed separately

Pattern	Model	Statistic	*All-plants*	*Wetland-only*	*Terrestrial*
Ranked species occupancy curve[a]	Symmetrical sigmoidal	a	–	1.404 [1.292, 1.547]	–
		b	–	−0.066 [−0.07, −0.063]	–
		c	–	−0.518 [−0.715, −0.308]	–
	Power exponential	y_0	0.011 [0.008, 0.014]	–	0.025 [0.021, 0.029]
		a	0.925 [0.914, 0.937]	–	0.852 [0.824, 0.880]
		b	0.032 [0.032,0.033]	–	0.108 [0.102, 0.114]
Species-area relationship	Power-law	c	23.8 [21.4, 26.4]	16.0 [14.3, 17.7]	8.3 [6.8, 9.8]
		z	0.21 [0.15, 0.27]	0.21 [0.15, 0.28]	0.20 [0.09, 0.31]
		R^2	0.39	0.40	0.16
Distance-decay in similarity[a]	Power-law	a	0.39 [0.38, 0.40]	0.44 [0.43, 0.46]	0.30 [0.28, 0.31]
		b	−0.13 [−0.14,−0.12]	−0.12 [−0.13, −0.11]	−0.16 [−0.18 −0.14]
		R^2	0.12	0.11	0.07

For all patterns estimated model coefficients and 95 % confidence intervals are shown. For species-area and distance-decay models, and index of goodness of fit (coefficient of determination R^2) is shown. For ranked species occupancy curves and distance decay, only the top-ranked model is given (Akaike's information criterion weights [*w*AIC] for all top-ranked models >0.99). Full model ranking results are in Appendix 5 of the Supplementary Information)

[a] Results for top-ranked model shown only—see Supplementary Information Tables A-7 and A-8 for all model rankings; see Jenkins (2011) and Hui (2012) for ranked species occupancy curve model formulae

Fig. 4 Species-area relationships for *all plants* (**a**) and *wetland-only* (**b**) datasets. The log–log implementation of the power-law species-area model is fitted to each data subset and the value for the intercept (*c*) slope parameter (*z*) and coefficient of determination (R^2) are shown in the bottom right of each panel

datasets (0.21) and were also equal to the mean *z*-value from previously published studies fitting power-law species-area relationships to similar shallow-wetland systems (mean [± 95 % confidence limits] = 0.21 [0.16, 0.27], *n* = 8; Table A-2, Appendix 2).

Average compositional turnover was higher in the *all plants* dataset ($\beta_1 = 0.09$) than the *wetland-only* dataset ($\beta_1 = 0.06$), due largely to the high turnover among *terrestrial* species ($\beta_1 = 0.17$) (Table 1). The values for the *all plants* and *wetland-only* communities were both low compared with the distribution of β_1 estimated from previously published studies, but for *terrestrial* communities considered separately, it was above the mean value (mean [±95 % confidence limits] = 0.15 [0.11, 0.19], *n* = 14; Tables A-4, A-5).

The top-ranked distance-decay model under all community definitions was the power-law with *w*AIC ≈ 1 in all cases. There was no difference in distance-decay comparing *wetland-only* and *all plants* communities, but the estimate for the slope (*b*) parameter of the distance-decay relationship was more negative among upland communities (mean [± 95 % confidence limits] = −0.127 [−0.139, −0.115], −0.117 [−0.128, −0.105] and −0.160 [−0.179, −0.140] for *all plants, wetland-only* and *terrestrial* communities, respectively; Fig. 5; Table 2; Fig. A-6, Table A-8 Appendix 4). The coefficient of determination in all distance-decay models was low (R^2 *all plants* = 0.11, *wetland-only* = 0.10). Wetlands with the most similar community composition tended to be located within the same catchment (Fig. 5, although this is clearer in Fig. A-6), although dissimilar wetlands were also present.

Total nestedness (i.e., considering both site composition and species occupancy) did not differ from null-model expectations for *wetland-only* or *terrestrial* communities ($p = 0.20$ and 0.44, respectively), but within *all plants* communities there was weak evidence of anti-nesting ($Z = -1.3$; $p = 0.10$; Table 3). This was largely a result of weak anti-nestedness in *terrestrial* occupancy; that is, rare *terrestrial* species were found less often than expected in the same wetlands as common species ($Z = -1.4$, $p = 0.08$; Table 3). Nestedness in *wetland-only* community composition was lower than null-model expectations, also
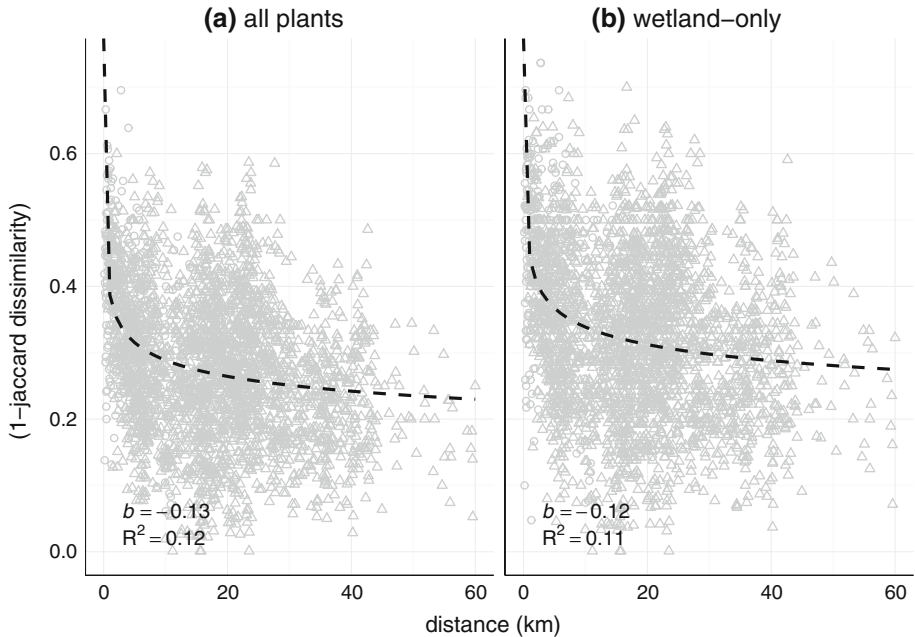
Fig. 5 Species turnover as a function of geographical distance (distance-decay) for *all plants* (**a**) and *wetland-only* (**b**) datasets modelled with a power function. Symbols denote wetlands in the same catchment (*open circles*) or different catchments (*open triangles*). The *y-axis* indicates the similarity in species composition between wetlands (measured as 1-Jaccard dissimilarity index), with higher values indicating more similar wetland communities. Also shown are the slope (*b*) and coefficient of determination (R^2) for the fitted models

Table 3 Nestedness analysis for the two datasets based on overlap and decreasing fill metrics (NODF)

Dataset	NODF[a]	Estimate[b]	Expected[c]	Z	P_Z
All plants	Total	28.79	29.89	−1.28	0.099
	Sites	51.37	52.13	−0.55	0.291
	Species	25.99	27.13	−1.35	0.089
Wetland-only	Total	47.34	48.65	−0.84	0.200
	Sites	56.00	58.67	−1.70	0.045
	Species	41.44	41.83	−0.21	0.416
Terrestrial	Total	23.41	23.27	0.15	0.442
	Sites	44.12	41.51	1.11	0.133
	Species	15.67	16.46	−1.39	0.083

Evidence of nestedness is indicated by estimates > expected under null community simulations, while estimates < expected indicate anti-nesting—the tendency for rare species not to occur with common species. Z-transform indicates how likely the result would be under the null hypothesis of no nestedness. The matrix fill values were 0.14, 0.22 and 0.08 for *all plants, wetland-only* and *terrestrial* communities respectively

[a] Nestedness metric based on the overlap and decreasing fill algorithm (Almeida-Neto et al. 2008); [b] NODF metric; [c] Mean NODF calculated from 999 simulated communities using the proportional–proportional re-shuffling algorithm (Almeida-Neto and Ulrich 2011)

suggesting anti-nestedness. In other words, the composition of species-poor wetlands were *not* comprised of subsets of species-rich wetlands more often than expected ($Z = -1.7$; $p = 0.05$; Table 3). There was also little evidence of nesting in species composition by wetland area (Table A-6, Appendix 4). The minimum percentage of the number of wetlands required to include every native plant species in at least one wetland was 49 % (59 % of total area), while for *wetland-only* plants this was 24 % of the total number (39 % of total area).

Discussion

Terrestrial species were a large and important component of total plant biodiversity, representing more than half of the species present in our dataset. The inclusion of terrestrial species changed occupancy distributions to a strongly unimodal pattern dominated by rare (satellite) species. This suggests that wetlands offer habitat for many rare terrestrial species and this increases species turnover. Nestedness analysis suggests rare terrestrial species were often found at different sites to more common ones; to include every native species in at least one wetland requires twice the number of wetlands, and 50 % more wetland area, than is needed for *wetland-only* species.

We show that the occupancy frequency distributions for *all plants* and *wetland–only* plants differed largely due to the rare terrestrial species. The *all plants* distribution was strongly unimodal, dominated by rare (satellite) terrestrial species, while the *wetland-only* distribution was more uniform in distribution as observed in histograms of the data (online Appendix I). The two top-ranked occupancy regression models provide statistical confirmation of these different distributions; the concave exponential model, top-ranked for *all plants,* is associated with a strongly unimodal satellite distribution and the sigmoidal symmetric model is associated with a bimodal distribution (Hui 2012; Jenkins 2011). Jenkins (2011) proposed different causal mechanisms for these two occupancy models, with dispersal limitation or high disturbance leading to an exponential concave model, and habitat heterogeneity and moderate disturbance resulting in sigmoidal patterns. However, our distance decay result suggests *wetland-only* species were *less* dispersal limited than terrestrial species meaning this is an unlikely explanation for the superior fit of the exponential concave model. Similarly the intensity of disturbance in wetland fringes where terrestrial species are more abundant is more likely to be greater, not more moderate as required for a sigmoidal occupancy model fit for *all-plants* under Jenkin's (2011) suggestions. We therefore confirm that occupancy distributions are not reliable indicators of biological mechanisms (Brown 1984; Hui 2012; McGeoch and Gaston 2002).

We hypothesised that reliance on hydrological niches would create nested patterns in *wetland-only* communities, but in fact found the opposite: *wetland-only* site-based species patterns were anti-nested—species-poor wetlands were *less* likely to be composed of subsets of species-rich wetlands than null models predict. In contrast, when terrestrial species were included, we found no evidence of anti-nesting among *sites*, but some suggestion that species *occupancies* were anti-nested. Anti-nestedness for species occupancies tends to occur when endemic species (here we refer to regional endemicity, which we define as those species observed in only one wetland) are not found at those sites where widespread species occur (Almeida-Neto et al. 2008). While high nestedness has been found previously for sedge meadows in Illinois, USA (Matthews 2004), Matthews et al. (2015) found that anti-nestedness was more frequently observed in habitat islands such as

wetlands, suggesting earlier work might be unreliable because of the metrics and null models adopted.

In our case the pattern largely arose because many of terrestrial species (39 %) were only present at one wetland, preventing nested patterns from forming (Almeida-Neto et al. 2008; Matthews et al. 2015). The practical implication of this is that a large proportion of wetland patches and total area are necessary to ensure that all species are conserved within the landscape (Matthews et al. 2015). To include every native species would require 59 % of wetlands by area and 49 % by number, and would need to include wetlands of all sizes. However, acting to protect this number of wetlands to provide terrestrial species habitat might be of limited practical conservation value. Since much of the region was only cleared during the 1950s, terrestrial species distributions could still be relaxing to the newly cleared landscape's spatial configuration of suitable and unsuitable patches (and their connectedness), meaning that they might actually represent a regional extinction debt (Diamond 1972; Tilman et al. 1994). Hence, whether wetlands would represent viable long-term habitat for these isolated populations is questionable.

Observed power-law behaviour ($z = 0.21$) for our wetland species was typical for habitat isolates such as islands (Drakare et al. 2006; Rosenzweig 1995; Triantis et al. 2012), and equal to the average of published results for similar wetland systems. The similarity in z parameter estimates between *all plants* and *wetland-only* communities is slightly at odds with prior studies separating terrestrial and wetland plants in seasonal wetlands. Both Brose (2001) and Smith and Haukos (2002) found that log–log transformed power-law species-area slopes decreased by up to 50 % when terrestrial plants were included, suggesting that terrestrial plants species were more widely distributed than wetland plants. In our case we found the opposite. Additionally, the low habitat heterogeneity of the Playa wetlands of the Southern Great Plains in the USA (Smith and Haukos 2002), or the high physical disturbance in temporary eastern German wetlands (Brose 2001) could have affected conclusions.

Species turnover as determined by the β_1 index was, as we anticipated, lower for *wetland-only* plant communities and also lower than previously published results (Table A-5, Appendix 3). The difference between *all plants* and *wetland-only* communities was however due to the greater turnover among terrestrial communities, which were high compared to prior studies. Similarly, slopes of the power-law distance-decay model indicated that similarity in composition in *terrestrial* communities decayed more rapidly than in *wetland-only* communities. Fleurieu wetlands are almost invariably associated with watercourses (Fig. 1), and increased intra-catchment similarity suggests hydrochory is an influential determinant of community composition. Hydrochory contributes to the maintenance of wetland plant species richness, but is also a vector for the spread of invasive species and can make wetlands more susceptible to climate change through its effects on streamflow patterns (Nilsson et al. 2010). This appears to be the reason that the top-ranked model was the power-law, although this has not been as widely applied to model distance-decay relationships as the other models we applied (Nekola and White 1999; Soininen et al. 2007).

We found that removing sampling bias for wetland databases presents a different challenge than for continuous biomes that can be represented with a grid because of the differences in area and possibly due to hydrological heterogeneity (Appendix 1, Online Resource 1). This has important implications for the future use of wetland survey databases because sampling effort (e.g. number of records, Hortal et al. 2007) might be an unreliable indicator of complete censuses in wetlands.

Our analysis indicates that the diversity of Fleurieu wetland plant communities depends largely on the community definition adopted; including terrestrial species changes conclusions on the diversity and variability in community composition. Including terrestrial species within the definition of the wetland plant community greatly increases both the number and area of wetlands necessary to include every species within at least one wetland. In our study region, wetland hydrology is such that terrestrial species can be found throughout the wetland extent in all but the wettest areas. However, in cleared landscapes even if wetlands form deeper-water habitat that precludes terrestrial species, wetland fringes might still provide suitable remnant habitat. As a result, particularly in modified landscapes, we recommend that terrestrial species be included in studies of the biodiversity associated with wetland habitat.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Almeida-Neto M, Ulrich W (2011) A straightforward computational approach for measuring nestedness using quantitative matrices. Environ Model Softw 26:173–178. doi:10.1016/j.envsoft.2010.08.003

Almeida-Neto M, Guimaraes P, Guimaraes PR, Loyola RD, Ulrich W (2008) A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. Oikos 117:1227–1239. doi:10.1111/j.0030-1299.2008.16644.x

Anderson MJ et al (2011) Navigating the multiple meanings of beta diversity: a roadmap for the practicing ecologist. Ecol Lett 14:19–28. doi:10.1111/j.1461-0248.2010.01552.x

Arrhenius O (1921) Species and area. J Ecol 9:95–99. doi:10.2307/2255763

Balian EV, Segers H, Leveque C, Martens K (2008) The freshwater animal diversity assessment: an overview of the results. Hydrobiologia 595:627–637. doi:10.1007/s10750-007-9246-3

Baselga A, Orme D, Villeger S, De Bortoli J, Leprieur F (2013) Betapart: partitioning beta diversity into turnover and nestedness components, R package version 1.3. edn

Brock MA, Casanova MT (1997) Plant life at the edges of wetlands: ecological responses to wetting and drying patterns. In: Klomp N, Lunt I (eds) Frontiers in ecology: building the links. Elsevier, Oxford, pp 181–192

Brose U (2001) Relative importance of isolation, area and habitat heterogeneity for vascular plant species richness of temporary wetlands in east-German farmland. Ecography 24:722–730. doi:10.1034/j.1600-0587.2001.240610.x

Brown JH (1984) On the relationship between abundance and distribution of species. Am Nat 124:255–279. doi:10.1086/284267

Burnham K, Anderson D (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York

Casanova MT (2011) Using water plant functional groups to investigate environmental water requirements. Freshw Biol 56:2637–2652. doi:10.1111/j.1365-2427.2011.02680.x

Casanova MT, Brock MA (2000) How do depth, duration and frequency of flooding influence the establishment of wetland plant communities? Plant Ecol 147:237–250. doi:10.1023/a:1009875226637

Chambers PA, Lacoul P, Murphy KJ, Thomaz SM (2008) Global diversity of aquatic macrophytes in freshwater. Hydrobiologia 595:9–26. doi:10.1007/s10750-007-9154-6

Clark R, Teoh K, Kotz S (2007) Surface water assessment for the southern Fleurieu region, DWLBC report 2009/05. Government of South Australia, through Department of Water, Land and Biodiversity Conservation, Adelaide

Davis J, Sim L, Chambers J (2010) Multiple stressors and regime shifts in shallow aquatic ecosystems in antipodean landscapes. Freshw Biol 55:5–18. doi:10.1111/j.1365-2427.2009.02376.x

Delgado M, Fajardo W, Gibaja E, Perez-Perez R (2005) BioMen: an information system to herbarium. Expert Syst Appl 28:507–518. doi:10.1016/j.eswa.2004.12.012

Diamond JM (1972) Biogeographic kinetics—estimation of relaxation-times for avifaunas of southwest Pacific islands. Proc Natl Acad Sci USA 69:3199. doi:10.1073/pnas.69.11.3199

Drakare S, Lennon JJ, Hillebrand H (2006) The imprint of the geographical, evolutionary and ecological context on species-area relationships. Ecol Lett 9:215–227. doi:10.1111/j.1461-0248.2005.00848.x

Dudgeon D (2010) Prospects for sustaining freshwater biodiversity in the 21st century: linking ecosystem structure and function. Curr Opin Environ Sustain 2:422–430. doi:10.1016/j.cosust.2010.09.001

Duffield R et al (2000) Nomination for listing the Fleurieu Peninsula Swamps as an Endangered Ecological Community under Section 181 of the Environment Protection and Biodiversity Conservation Act 1999. Conservation Council of South Australia and the Nature Conservation Society of South Australia, Adelaide

Elith J et al (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129–151. doi:10.1111/j.2006.0906-7590.04596.x

Elzhov T, Mullen K, Spiess A, Bolker B (2015) Minpack.lm: R interface to the Levenberg–Marquardt nonlinear least-squares algorithm, R package version 1.2-0

Fauth JE, Bernardo J, Camara M, Resetarits WJ, VanBuskirk J, McCollum SA (1996) Simplifying the jargon of community ecology: a conceptual approach. Am Nat 147:282–286. doi:10.1086/285850

Fordham DA et al (2012) Plant extinction risk under climate change: are forecast range shifts alone a good indicator of species vulnerability to global warming? Glob Change Biol 18:1357–1371. doi:10.1111/j.1365-2486.2011.02614.x

Graham CH, Ferrier S, Huettman F, Moritz C, Peterson AT (2004) New developments in museum-based informatics and applications in biodiversity analysis. Trends Ecol Evol 19:497–503. doi:10.1016/j.tree.2004.07.006

Harding CL (2005) Wetland inventory for the Fleurieu Peninsula. Department for Environment & Heritage, Adelaide

Harrison S, Ross SJ, Lawton JH (1992) Beta-diversity on geographic gradients in Britain. J Anim Ecol 61:151–158. doi:10.2307/5518

Haukos DA, Smith LM (1994) The importance of Playa wetlands to biodiversity of the Southern High Plains. Landsc Urb Plan 28:83–98. doi:10.1016/0169-2046(94)90046-9

Holland CC, Honea JE, Gwin SE, Kentula ME (1995) Wetland degradation and loss in the rapidly urbanizing area of Portland. Or Wetl 15:336–345

Hortal J, Lobo JM, Jimenez-Valverde A (2007) Limitations of biodiversity databases: case study on seed-plant diversity in Tenerife. Canary Isl Conserv Biol 21:853–863. doi:10.1111/j.1523-1739.2007.00686.x

Houlahan JE, Keddy PA, Makkay K, Findlay CS (2006) The effects of adjacent land use on wetland species richness and community composition. Wetlands 26:79–96

Hui C (2012) Scale effect and bimodality in the frequency distribution of species occupancy. Community Ecol 13:30–35. doi:10.1556/ComEc.13.2012.1.4

Jenkins DG (2011) Ranked species occupancy curves reveal common patterns among diverse metacommunities. Glob Ecol Biogeogr 20:486–497. doi:10.1111/j.1466-8238.2010.00617.x

Kaeser MJ, Kirkman LK (2009) Estimating total plant species richness in depressional wetlands in the Longleaf Pine ecosystem. Wetlands 29:866–874

Lastrucci L, Landi M, Angiolini C (2010) Vegetation analysis on wetlands in a Tuscan agricultural landscape (central Italy). Biologia 65:54–68. doi:10.2478/s11756-009-0213-5

Lobo JM (2008) Database records as a surrogate for sampling effort provide higher species richness estimations. Biodivers Conserv 17:873–881. doi:10.1007/s10531-008-9333-4

Matthews JW (2004) Effects of site and species characteristics on nested patterns of species composition in sedge meadows. Plant Ecol 174:271–278. doi:10.1023/B:VEGE.0000049107.11273.cb

Matthews TJ, Cottee-Jones HEW, Whittaker RJ (2015) Quantifying and interpreting nestedness in habitat islands: a synthetic analysis of multiple datasets. Divers Distrib 21:392–404. doi:10.1111/ddi.12298

McGeoch MA, Gaston KJ (2002) Occupancy frequency distributions: patterns, artefacts and mechanisms. Biol Rev Camb Philos Soc 77:311–331. doi:10.1017/S1464793101005887

Nekola JC, White PS (1999) The distance decay of similarity in biogeography and ecology. J Biogeogr 26:867–878. doi:10.1046/j.1365-2699.1999.00305.x

Nilsson C, Brown RL, Jansson R, Merritt DM (2010) The role of hydrochory in structuring riparian and wetland vegetation. Biol Rev 85:837–858. doi:10.1111/j.1469-185X.2010.00129.x

Oksanen J et al (2013) vegan: community ecology package. R package version 2.0-10

R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Reed PBJ (1988) National list of plant species that occur in wetlands: national summary. US Fish Wildlife Service. Biol Rep 88(24):244

Rodrigues ASL, Gaston KJ (2001) How large do reserve networks need to be? Ecol Lett 4:602–609. doi:10.1046/j.1461-0248.2001.00275.x

Rosenzweig ML (1995) Species diversity in space and time. Cambridge University Press, New York

Smith LM, Haukos DA (2002) Floral diversity in relation to playa wetland area and watershed disturbance. Conserv Biol 16:964–974. doi:10.1046/j.1523-1739.2002.00561.x

Soberon J, Peterson AT (2004) Biodiversity informatics: managing and applying primary biodiversity data. Philos Trans Royal Soc Lond Ser B 359:689–698. doi:10.1098/rstb.2003.1439

Soininen J, McDonald R, Hillebrand H (2007) The distance decay of similarity in ecological communities. Ecography 30:3–12. doi:10.1111/j.2006.0906-7590.04817.x

Tilman D, May RM, Lehman CL, Nowak MA (1994) Habitat destruction and extinction debt. Nature 371:65–66. doi:10.1038/371065a0

Tjørve E (2003) Shapes and functions of species-area curves: a review of possible models. J Biogeogr 30:827–835. doi:10.1046/j.1365-2699.2003.00877.x

Triantis KA, Guilhaumon F, Whittaker RJ (2012) The island species-area relationship: biology and statistics. J Biogeogr 39:215–231. doi:10.1111/j.1365-2699.2011.02652.x

Ulrich W, Gotelli NJ (2012) A null model algorithm for presence–absence matrices based on proportional resampling. Ecol Model 244:20–27. doi:10.1016/j.ecolmodel.2012.06.030

von Behren C, Dietrich A, Yeakley JA (2013) Riparian vegetation assemblages and associated landscape factors across an urbanizing metropolitan area. Ecoscience 20:373–382. doi:10.2980/20-4-3635

Whittaker RH (1960) Vegetation of the Siskiyou Mountains. Or Calif Ecol Monogr 30:280–338

Wickham H (2007) Reshaping data with the reshape package. J Stat Softw 21:1–20

Wickham H (2009) ggplot2: elegant graphics for data analysis. Springer, New York

Wilson D, Paton DC (2004) Habitat use by the Southern Emu-wren, *Stipiturus malachurus* (Aves: Maluridae), in South Australia, and evaluation of vegetation at a potential translocation site for S-m. intermedius. Emu 104:37–43. doi:10.1071/mu01054