Quantifying Biodiversity Patterns and Extinction Risk in

Seasonal Wetland Plant Communities

by

David Charles Deane B.Sc.

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Acknowledgements

Abstract

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David Deane

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Supervisors: Corey J A Bradshaw

Damien A. Fordham

Fangliang He

Wetlands are among the most threatened habitats on Earth. They are essential components of functional landscapes, providing habitat for native flora and fauna as well as supporting critical ecosystem services. Loss of wetland biodiversity threatens these values. There is an urgent need to understand patterns of wetland biodiversity, the processes creating these and the risk of species loss to plan effective intervention. Species-area relationships have a successful, although controversial, history of quantifying the risk of extinction in terrestrial biomes, and can provide rapid estimates of extinction risk at a range of scales without the need for extensive datasets. Prior to my research, applications of species-area relationships in extinction risk were limited to island archipelagos and formerly continuous terrestrial habitats that had become fragmented. Naturally occurring, discrete habitat types—such as wetlands—have been ignored. I address this gap, demonstrating that area-based methods can, with some modification, be successfully applied to predict extinction risk in wetland communities. Before considering extinction risk I analysed patterns of wetland plant diversity and occupancy and how competing community-assembly processes produce more or less unique combinations of species among wetlands. I showed that much of the plant community diversity in seasonal wetlands in South Australia is driven by rare terrestrial

species of wetland fringes, which assemble from a much larger available species pool. The distribution of these rare species was not correlated with total species richness or wetland size, suggesting that changes in the number or total area of wetlands could result in different extinction dynamics, depending on how they affected endemic species. I therefore compared risks associated with loss of complete wetlands (patch loss), with loss of the equivalent wetland area while maintaining the total number of wetlands. To implement the latter scenario, I developed a novel approach consisting of three steps: (*i*) a generalized empirical endemics-area relationship to predict the number of species lost within each wetland as a function of a reduction in wetland area; (*ii*) I selected the identities of the predicted number of species lost at each wetland probabilistically; (*iii*) I compred the number of wetlands from which each species was lost with its regional occupancy, and I considered any species predicted to be lost from all known sites as extinct. I then repeated steps (*ii*) and (*iii*) many times to obtain a distribution of regional-scale species loss for a given loss of area in each wetland. Step (*ii*) allowed for different scenarios to be tested by adjusting the sampling probability for each species. I found that a higher extinction risk was associated with the loss of complete wetlands than the equivalent area loss shared among all wetlands. Moreover, for a given area loss, small wetlands had a much higher risk of species loss due to the distribution of endemic species. The approach I developed could be readily applied to any discrete habitat type, providing predictions of risk for a range of ecosystems that have received little attention.

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Context of research

In this thesis I consider the question of wetland biodiversity conservation, explicitly from the perspective of area-based extinction-risk assessments of wetland plant communities. Following a brief review of relevant concepts to set the scene in Chapter 1, I present the main body of research as a series of three chapters formatted for publication:

- In Chapter 2, I use a large database to examine variation in ecological patterns, comparing geographic- and assemblage-based definitions of the wetland plant community. I show that terrestrial species are a diverse and variable component of seasonal wetlands, and in cleared landscapes can provide an important reservoir of native biodiversity for all plants. The implication of the narrow distribution of many terrestrial plants raises the extinction risk associated with any process that decreases total wetland area. However, if rare terrestrial species were distributed as a result of heterogeneity in environmental conditions, then extinction risk would increase with the loss of that heterogeneity rather than area.

- In Chapter 3 I test three predictions on the assembly mechanisms structuring wetland plant communities, specifically seeking to understand what makes some wetland plant communities more regionally unique in species composition than others. I considered niche, dispersal and competition based mechanisms and found evidence suggesting that all three contribute to wetland plant community diversity. Unique species compositions arise as a trade-off between productive conditions and competitive exclusion. I found evidence that landscape context affects the competitive environment, especially over short distances ($\sim$ 400 m).

- Having determined that (*i*) rare terrestrial plants are an important component of these seasonal wetlands, and (*ii*) their distribution does not arise from environmental determinism (niche-based processes) alone, I concluded that area loss represents the

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major risk of extinction. In Chapter 4 I compared two possible trajectories: loss of

entire wetlands (patch loss) and loss of an equivalent amount of area while retaining

patch number (area loss). To determine the risk associated with area loss, I

developed a novel application of the endemics-area relationship. This analysis

showed that the risk of species extinction is greater for patch loss than the loss of an

equivalent area distributed across all wetlands.

Finally in Chapter 5, I consider the implications of this body of research, discussing its

significance along with the technical and other problems I encountered. I also suggest some

future directions for the work.

Chapter 1   Wetland Biodiversity Conservation and Area-based Methods for Extinction Prediction

Introduction

In little over 100 years, global wetland area has been reduced to around one-third of what it was in 1900, declining on average at a rate exceeding 1% year^{-1} (Davidson, 2014), yet the number of species going extinct as a result of this habitat loss remains unknown. The proportional risk of extinction for freshwater biota is thought to be higher than for almost any other group (Dudgeon et al., 2006, Balian et al., 2008), a consequence of both high diversity and endemicity (Dudgeon et al., 2006, Balian et al., 2008) and the multiple stressors imposed by human activities (Dudgeon 2010). In North America for example, the projected extinction rate for freshwater fauna exceeds that of terrestrial fauna by a factor of five (Revenga et al., 2005), a problem amplified by the poor coverage afforded to freshwater ecosystems under existing protected area networks (Heino et al., 2009, Darwall et al., 2011, Williamson et al., 2013). There is thus a clear and urgent need for action to understand these extinction risks and to conserve freshwater biodiversity (Dudgeon, 2010, Strayer and Dudgeon, 2010), but this presents many practical and scientific challenges.

Perhaps the most difficult issue is reconciling the basic human need for water security with the needs of biodiversity. Areas of low water security, expanding populations and high biodiversity tend to be correlated (Vörösmarty et al., 2010) and humans will always assign a higher priority to their water supplies. Climate change impacts on both biodiversity and water resources brings additional pressures and uncertainties to conservation. Strayer and Dudgeon (2010) highlighted the risk to freshwater systems from mitigation strategies focused on engineering solutions to address climate change; they recommended that predictive modelling of possible outcomes is important to guide such

developments. But the availability of suitable modelling methods presents a major impediment to developing effective mitigation strategies, particularly as freshwater biodiversity research lags behind that of terrestrial systems (Abell, 2002, Balian et al., 2008, Darwall et al., 2011). While Stendera et al. (2012) found species-area relationships to be the second-most commonly tested pattern relating to freshwater biodiversity, its use in freshwater research has been largely descriptive. In contrast, terrestrial ecologists have used species-area relationships to predict patterns of extinction in the fossil record since the 1970s (e.g., Simberloff, 1974) and over timeframes for around 20 years (e.g., Brooks et al., 1997, Pandit et al., 2007, Koh and Ghazoul, 2010). To date, Giam et al. (2012) provide the only comparable application in the freshwater domain, investigating freshwater fish extinction risk from loss of riverine habitat area.

The species-area relationship in extinction prediction

Interest in species-area-based explanations of extinction originated with the development of MacArthur and Wilson's (1967) equilibrium theory of island biogeography (Boecklen and Simberloff, 1986). Island biogeography states that for a given area and degree of isolation, island diversity represents a balance between speciation (or immigration) and extinction rates. Extinction rates in smaller areas increase because they hold fewer individuals, thus increasing the risk these could all be lost due to random events. This general theory provided a plausible explanation for the observation over geological timescales that some mass extinction events coincided with changes in sea level that altered the available marine and terrestrial habitable areas (Boecklen and Simberloff, 1986). Simberloff (1974) was the first to test the richness-area relationship empirically, finding the relationship between the number of marine invertebrate families and the area of marine habitat resulting from sea level change through the Permian and Lower Triassic period were linear in log-log space (as earlier suggested by Schopf, 1974).

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The use of species-area relationships to predict extinction over ecological timescales began with Pimm and Askins (1995), who attempted to explain bird species losses as a result of reductions in North American forest area using the power-law formulation of the species-area relationship attributed to Arhennius (1920):

$$s = C \cdot A^z \qquad\qquad 1$$

where s is the total number of species; A is the area and C and z are fitting constants (Connor and McCoy, 1979). In applications of the power-law species-area relationship (e.g. Pimm and Askins, 1995, Brooks et al., 1997), the exponent z was used to scale the remaining species and area fractions according to:

$$\frac{S_{new}}{S_{org}} = \frac{A_{new}}{A_{org}}^z \qquad\qquad 2$$

where S_{new} and S_{org} are the number of species in the remaining and original areas (A_{new} and A_{org}), respectively. The value selected for the scaling factor (z) was usually based either on a species-area relationship fitted to the post-change landscape, or based on the 'canonical' value of 0.262 (although 0.25 is more commonly used) derived theoretically for habitat isolates by Preston (1962). Both of these approaches for assigning z are now out of favour (Smith, 2010, He and Hubbell, 2011, Gerstner et al., 2014).

Criticism of this approach, which came to be known as the 'backward species-area method', included the perception that it over-estimated actual species extinctions (Heywood and Stuart, 1992, Heywood et al., 1994, May et al., 1995), although this too has recently been challenged (Fattorini and Borges, 2012, Rybicki and Hanski, 2013, Halley et al., 2014). Further criticisms noted that predictions did not account for the differential survival potential that can arise, even for closely related species, in the post-change habitat matrix (Ricketts, 2001, Laurance, 2008). Recently there has been a trend to create more complex species-area formulae to account for differential matrix survival probabilities among species as well as variation in geographical range size, degrees of habitat fragmentation and

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habitat heterogeneity in species-area relationships (Ney-Nifle and Mangel, 2000, Triantis et al., 2003, Pereira and Daily, 2006, Koh et al., 2010, Hanski et al., 2013). However, there is currently no consensus on which model provides the best predictive performance.

An alternative area-based method that models the distribution of endemic-species has also been explored (Harte and Kinzig, 1997, Kinzig and Harte, 2000, Harte et al., 2005). The appeal of using endemic, rather than all species arises because of their narrow geographic distributions. Endemic species will inevitably go extinct if the reduction in area includes their entire population (Sodhi et al., 2009) and therefore the use of endemic species should produce reliable estimates of immediate extinction due to the lost area. The original endemics-area relationship was derived theoretically based on an assumption that patterns of endemic species distributions are essentially fractal and represent a pattern that repeats itself at every scale (Harte and Kinzig, 1997). The Harte and Kinzig (1997) model has been used in several biodiversity studies (Ulrich, 2005, Malcolm et al., 2006), despite the prior demonstration that the method has poor predictive performance (Green et al., 2003).

Area-based extinction prediction methods were later re-defined by He and Hubbell (2011), who derived a completley general sampling theory for species-area relationships that had previously been lacking. They identified that the difference between the area of 'first encounter' and that of the 'last encounter' produces a systematic bias, as had been alluded to in a qualitative sense by Smith (2010). The critical point relates to the complementarity of the area removed and the area remaining. If species are randomly distributed, the first encounter and last encounter areas are complementary and sum to that of the whole study area; but when species are not randomly distributed, the sum of the two areas is smaller than the whole study area and this difference results in an overestimation using the backward species-area method (He and Hubbell 2011). The area required to

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include every individual of a species and lead to its extinction is what is predicted by the endemics-area relationship. Using empirical endemics-area relationships based on stem-mapped forest data, He and Hubbell showed this relationship was almost perfectly predicted using the random placement analytical formula for the endemics-area relationship derived by Green and Ostling (2003) from the equivalent species-area formulae of He and Legendre (2002). Although subject to strong criticism (e.g., Fattorini and Borges, 2012, Pereira et al., 2012, Axelsen et al., 2013), the findings of He and Hubbell (2011; further developed in He and Hubbell, 2013) have not been mathematically invalidated. The endemics-area relationship remains the most reliable method to predict the number of imminent extinctions that will occur given a loss of habitat area (He and Hubbell, 2011, He and Hubbell, 2013).

Biologically, it is widely known that imminent extinctions are only part of the extinction process when habitat area is reduced; an extinction debt follows fragmentation as species 'relax' into the new habitat geometry and some are reduced below minimum viable population size (Diamond, 1972, Tilman et al., 1994). Relaxation times have been predicted to involve periods that can be thousands of years for long-lived species (Diamond, 1972, Halley et al., 2014), potentially allowing time for conservation intervention (Kuussaari et al., 2009). In other systems, the relaxation period is in the order of decades or less (Gibson et al., 2013). In contrast, imminent extinctions are the unavoidable and immediate consequences of habitat loss. Quantifying the imminent extiction fraction as accurately as possible should be viewed as an important part of understanding the risk of extinction while recognising it is unlikely to represent the eventual, full impact.

Applying species-area relationships to wetlands

As discrete habitat patches nested within a hostile matrix, wetlands appear to have much in common with the fragmented habitats to which area-based extinction methods

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have been traditionally applied. However, such applications in wetlands are conspicuously absent from the literature. Published wetland studies have mostly used species-area relationships as a covariate to explain species richness, and they have never been used in a predictive sense. I reviewed 35 studies that applied species-area relationships to wetland plant communities, of which 75 % found evidence for a log-transformed power function species-area relationship with a positive slope (Tables 1.1 and 1.2). This suggests that species-area relationships could be useful for predicting extinction in wetlands in the same manner that they have been applied in other biomes. Although the explained variation in published species-area relationships for wetland plant communities differs considerably among studies (R^2 range: $7 - 95$ %), this is largely a function of the number of wetlands in the study and is also typical of species-area relationships in other biomes (Triantis et al., 2012). Thus, there appears to be no a priori reason to preclude area-based methods for predicting wetland extinctions.

Extinction risk research in wetland plant communities

Predicting the extinction risk of wetland plants has to date attracted little research interest using any method, perhaps because many wetland plants have wide geographical distributions (Santamaria, 2002). However, nearly 40 % of aquatic macrophytes are endemic to a single bioregion, and in the afro- and neo-tropics—where the highest global rates of wetland area losses are found (Davidson, 2014)—their endemicity exceeds 60 % (Chambers et al., 2008). Hence there seems a clear imperative to quantify the risks of global change on wetland plant communities.

Only three studies have considered the risk to wetland plant species diversity from a reduction in wetland area, and none of these made regional predictions. Rosset et al. (2010) used generalised linear models, incorporating wetland area as a covariate, to predict changes in species richness of alpine ponds, making predictions at the pond-scale. Two

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studies have used plot-based rarefaction—a form of species accumulation related to, but distinct from, the species-area relationship (Gotelli and Colwell, 2001, Ugland et al., 2003, Gray et al., 2004) to predict extinction risk of aquatic vegetation. Úbeda et al. (2013) investigated climate change risk to the Ibera wetlands, Argentina using vegetation data from two surveys 30 years apart to build and compare separate species-accumulation curves. These were used as a qualitative aid to the interpretation of hydrological model outputs. The authors concluded that there was little risk to plant species richness because the reduction in area predicted from hydrological modelling was small, while the area required to reach saturation in their asymptotic species-accumulation curve[1] was less than 1% of total area. Ström et al. (2012) used plot-based rarefaction curves to quantify change in riparian species zonation, and therefore richness, as a function of projected climate-induced shifts in flooding regime. They classified vegetation sampling plots into different zones on the basis of species composition, cover and elevation. They then determined species richness of each zone with the rarefaction curve and based post-change estimates on the proportion of sampling plots remaining within their preferred depth-duration range (indicated by elevation and the projected hydrograph). Therefore, no prior study has used existing species- or endemics-area based methods, and none has predicted species losses at scales exceeding individual wetlands.

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[1] They used a 3-parameter Chapman function: $S = a(1-e^{(-bA)})^c$, although parameters a and c were not estimated (fixed).

Table 1.1 summary statistics for published wetland, lake and pond studies using power-law species-area relationships. Studies above the double line were used to calculate mean wetland z-parameter values. Other studies were done in systems considered too dissimilar for meaningful comparison. Values from studies marked with an asterisk were fitted by us based on data presented.

Reference	country	wetland type	z-value[#]	R^{2}[##]
Rolon and Maltchik (2006)	Brazil	wetlands	0.09	10.2
Houlahan et al. (2006)	Canada	wetlands	0.16	58
Shi et al. (2010)	China	wetlands	0.19	49.4
Weiher (1999)	Canada	herbaceous marshes	0.20	94.5
Findlay and Houlahan (1997)*	Canada	wetlands	0.22	52
Smith and Haukos (2002)	US	playa wetlands	0.24	19.6
Brose (2001)	Germany	temporary wetlands	0.24	11
Rolon et al. (2008)	Brazil	wetlands	0.36	37.4
Peintinger et al. (2003)	Switzerland	calcareous fens	0.09	29.7
Macroberts and Macroberts (1992)	US	bogs	0.11	88.7
Matthews (2003)	US	mixed wetlands	0.13	7
Oertli et al. (2002)	Switzerland	ponds	0.07	6.6
Linton and Goulder (2000)	UK	ponds	0.12	4.8
Bronmark (1985)	Sweden	ponds	0.13	18.7
Gee et al. (1997)	UK	ponds	0.13	22
Friday (1987)*	UK	ponds	0.16	12.7
Ebert and Balko (1987)*	US	temporary ponds	0.17	30.5
Jackson and Charles (1988)*	US	ponds	0.17	40
Jeffries (1991)*	Scotland	pond incl. artificial	0.18	18.6
Moller and Rordam (1985)	Denmark	ponds	0.27	84.1
Moller and Rordam (1985)	Denmark	ponds	0.32	92.7
Thomaz et al. (2003)	Brazil	lakes	0.33	47
Weiher and Boylen (1994)	US	ponds and lakes	0.23	57

Table 1.2 Summary values from Table 1.1. Mean z-parameter and coefficient of determination values and 95 % confidence intervals for studies done in wetlands and all aquatic systems.

system under study	mean z value[#] [95 % CI]	R^{2}[##] [95 % CI]
wetlands	0.21 [0.159, 0.267]	41 [21.8, 61.2]
all aquatic systems	0.19 [0.154, 0.217]	38 [26.2, 49.4]

[#] the z-parameter value for the power-law species-area model; [##] coefficient of determination for the overall power-law species-area relationship fitted.

Rationale and motivation for this research

Recognising that:

1. wetlands are among the most important terrestrial biomes for both biodiversity (Dudgeon et al., 2006) and the provision of ecosystem services (Costanza et al., 1997);

2. there has been a massive decline in wetland area, with remaining wetlands now constituting only 29 to 36 % of the global area recorded at the turn of the 20th Century (Zedler and Kercher, 2005, Davidson, 2014);

3. demographic, economic and environmental trends suggest loss and degradation in both tropical (Junk, 2002) and temperate (Brinson and Malvarez, 2002) wetlands will continue or increase over coming decades;

4. developing areas of the world, where policy frameworks are most limited, are considered to be the most vulnerable to wetland loss (Brinson and Malvarez, 2002, Junk, 2002);

5. even in developed countries loss of wetland area continues, e.g., > 250,000 ha of forested wetland area was lost in the conterminous US between 2004 and 2009 (Dahl, 2011); and

6. policy frameworks that consider sustainable management of wetlands with a long-term integrated watershed view are lacking (Junk, 2002, Daniels and Cumming, 2008);

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There is therefore an urgent need to improve our understanding of the distribution of biodiversity in wetlands and predict the risk of extinction as a result of a loss of wetland area. The aim of my research was to develop predictive methods to inform policy evolution by developing models that quantify the likely effect of area reduction scenarios on wetland plant communities. Such methods will enable planners to evaluate the risks and benefits of different land use or global change scenarios when developing mitigation policies.

In this thesis I concentrate on native plant communities of wetlands on the Fleurieu Peninsula in South Australia. Wetlands in this region are noted for the numbers of species of conservation concern that use this habitat either permanently, seasonally or occasionally (Duffield et al., 2000, Harding, 2005). The most high-profile fauna species, although not an obligate wetland resident, is the critically endangered Stipiturus malarchus intermedia, the Mount Lofty Ranges southern emu-wren ((Duffield et al., 2000, Wilson and Paton, 2004). Calls for conservation of Fleurieu wetland ecosystems can be traced to the 1980s when a report into the conservation of native vegetation in the State found almost half of a large sample of plants of conservation significance in the southern Fleurieu region were confined to upland wetlands (Lang and Kraehenbuehl, 1987). Later efforts led to the successful nomination of a subset of Fleurieu Peninsula wetlands as a Threatened Ecological Community under the Environment Protection and Biodiversity Conservation Act 1999 with a status of Critically Endangered (Duffield et al., 2000). Despite this concern, there is still little known of the distribution of plant biodiversity, the different mechanisms that structure wetland plant communities or the risk of regional extinction for wetland plant species. I address these knowledge gaps in the following three chapters.

Hypotheses under test

- In Chapter 2, I use a large database to test the hypothesis that terrestrial species
  inhabiting wetland fringes and drier microhabitats alter patterns of wetland plant
  biodiversity. I define terrestrial species as those capable of surviving outside of the
  wetland environment and use an existing water plant functional group classification
  to divide full census inventories from a large wetland plant database into two datasets:
  one consisting of all plants, the other only obligate wetland species. To test my
  hypothesis, I fit a number of ecological models and scaling relationships to both
  datasets and compared estimates in coefficient values. I expected to see increases in
  β-diversity and distance decay and a increase in the slope values of species-area
  relationships with the inclusion of terrestrial plants because of their larger regional
  species pool.

- In Chapter 3 I seek to understand the reason that some wetlands comprise regionally
  unique species compositions, while others appear regionally similar. I test three
  hypotheses in this regard, each corresponding to different community assembly
  mechanisms (niche, competition and disperal controlled). Under an information
  theoretic inferential framework I built a candidate set of models using three model
  subsets, where each subset used only predictors corresponding to different assembly
  mechanisms. I compared predictor importance using model averaged regression
  coefficients, expecting that niche-based processes—particularly hydrological
  heterogeneity—would exert the dominant influence in species composition, by
  providing habitat conditions suited to a larger fraction of the regional species pool.

- In Chapter 4 I test the hypothesis that loss of entire wetlands (patch loss) would create
  a higher risk of regional extinction of plant species than the loss of an equivalent
  amount of area while retaining patch number (area loss). I removed patches in
  different size orderings (large to small; small to large; random) to test sensitivity to
  different loss scenarios. To compare risks associated with area loss with these patch
  loss predictions, I developed a novel application of the endemics-area relationship,

using it to predict wetland scale species loss, then selecting species identities probabilistically and comparing with regional occupancies to determine the number of regional species lost. I anticipated wetland patch losses would exceed area reduction losses if patch number was conserved, because of the number of satelite (occupying few wetlands) species in the regional pool.

References

ABELL, R. 2002. Conservation biology for the biodiversity crisis: A freshwater follow-up. *Conservation Biology,* 16**,** 1435-1437.

AXELSEN, J. B., ROLL, U., STONE, L. & SOLOW, A. 2013. Species-area relationships always overestimate extinction rates from habitat loss: comment. *Ecology,* 94**,** 761-763.

BALIAN, E. V., SEGERS, H., LEVEQUE, C. & MARTENS, K. 2008. The freshwater animal diversity assessment: An overview of the results. *Hydrobiologia,* 595**,** 627-637.

BOECKLEN, W. J. & SIMBERLOFF, D. 1986. Area-based extinction models in conservation. *In:* ELLIOT, D. K. (ed.) *Dynamics of extinction.* New York: John Wiley & Sons.

BRINSON, M. M. & MALVAREZ, A. I. 2002. Temperate freshwater wetlands: types, status, and threats. *Environmental Conservation,* 29**,** 115-133.

BRONMARK, C. 1985. Fresh-water snail diversity - effects of pond area, habitat heterogeneity and isolation. *Oecologia,* 67**,** 127-131.

BROOKS, T. M., PIMM, S. L. & COLLAR, N. J. 1997. Deforestation predicts the number of threatened birds in insular southeast Asia. *Conservation Biology,* 11**,** 382-394.

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.

CONNOR, E. F. & MCCOY, E. D. 1979. Statistics and biology of the species-area relationship. *American Naturalist,* 113**,** 791-833.

COSTANZA, R., DARGE, R., DEGROOT, R., FARBER, S., GRASSO, M., HANNON, B., LIMBURG, K., NAEEM, S., ONEILL, R. V., PARUELO, J., RASKIN, R. G.,

SUTTON, P. & VANDENBELT, M. 1997. The value of the world's ecosystem services and natural capital. *Nature,* 387**,** 253-260.

DAHL, T. E. 2011. Status and trends of wetlands in the conterminous United States 2004 to 2009 *In:* SERVICE, F. A. W. (ed.). Washington, D.C.: U.S. Department of the Interior.

DANIELS, A. E. & CUMMING, G. S. 2008. Conversion or conservation? Understanding wetland change in northwest Costa Rica. *Ecological Applications,* 18**,** 49-63.

DARWALL, W. R. T., HOLLAND, R. A., SMITH, K. G., ALLEN, D., BROOKS, E. G. E., KATARYA, V., POLLOCK, C. M., SHI, Y., CLAUSNITZER, V., CUMBERLIDGE, N., CUTTELOD, A., DIJKSTRA, K.-D. B., DIOP, M. D., GARCIA, N., SEDDON, M. B., SKELTON, P. H., SNOEKS, J., TWEDDLE, D. & VIE, J.-C. 2011. Implications of bias in conservation research and investment for freshwater species. *Conservation Letters,* 4**,** 474-482.

DAVIDSON, N. C. 2014. How much wetland has the world lost? Long-term and recent trends in global wetland area. *Marine and Freshwater Research,* 65**,** 934-941.

DIAMOND, J. M. 1972. Biogeographic kinetics - estimation of relaxation-times for avifaunas of southwest Pacific islands. *Proceedings of the National Academy of Sciences of the United States of America,* 69**,** 3199-&.

DUDGEON, D. 2010. Prospects for sustaining freshwater biodiversity in the 21st century: linking ecosystem structure and function. *Current Opinion in Environmental Sustainability,* 2**,** 422-430.

DUDGEON, D., ARTHINGTON, A. H., GESSNER, M. O., KAWABATA, Z. I., KNOWLER, D. J., LEVEQUE, C., NAIMAN, R. J., PRIEUR-RICHARD, A. H., SOTO, D., STIASSNY, M. L. J. & SULLIVAN, C. A. 2006. Freshwater

biodiversity: importance, threats, status and conservation challenges. *Biological Reviews,* 81**,** 163-182.

DUFFIELD, R., T., M., M., R. & B., H. 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*. Adelaide: Conservation Council of South Australia and the Nature Conservation Society of South Australia.

EBERT, T. A. & BALKO, M. L. 1987. Temporary pools as islands in space and in time - the biota of vernal pools in San Diego, southern California, USA. *Archiv Fur Hydrobiologie,* 110**,** 101-123.

FATTORINI, S. & BORGES, P. A. V. 2012. Species-area relationships underestimate extinction rates. *Acta Oecologica-International Journal of Ecology,* 40**,** 27-30.

FINDLAY, C. S. & HOULAHAN, J. 1997. Anthropogenic correlates of species richness in southeastern Ontario wetlands. *Conservation Biology,* 11**,** 1000-1009.

FRIDAY, L. E. 1987. The diversity of macroinvertebrate and macrophytes communities in ponds. *Freshwater Biology,* 18**,** 87-104.

GEE, J. H. R., SMITH, B. D., LEE, K. M. & GRIFFITHS, S. W. 1997. The ecological basis of freshwater pond management for biodiversity. *Aquatic Conservation-Marine and Freshwater Ecosystems,* 7**,** 91-104.

GERSTNER, K., DORMANN, C. F., VACLAVIK, T., KREFT, H. & SEPPELT, R. 2014. Accounting for geographical variation in species-area relationships improves the prediction of plant species richness at the global scale. *Journal of Biogeography,* 41**,** 261-273.

GIAM, X. L., KOH, L. P., TAN, H. H., MIETTINEN, J., TAN, H. T. W. & NG, P. K. L. 2012. Global extinctions of freshwater fishes follow peatland conversion in Sundaland. *Frontiers in Ecology and the Environment,* 10**,** 465-470.

GIBSON, L., LYNAM, A. J., BRADSHAW, C. J. A., HE, F., BICKFORD, D. P., WOODRUFF, D. S., BUMRUNGSRI, S. & LAURANCE, W. F. 2013. Near-Complete Extinction of Native Small Mammal Fauna 25 Years After Forest Fragmentation. *Science,* 341**,** 1508-1510.

GILBERT, F. S. 1980. The equilibrium theory of island biogeography - fact or fiction. *Journal of Biogeography,* 7**,** 209-235.

GOTELLI, N. J. & COLWELL, R. K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters,* 4**,** 379-391.

GOTELLI, N. J. & GRAVES, G. R. 1996. *Null models in ecology*, Smithsonian Institution Press, Suite 2100, 955 L'Enfant Plaza, Washington, DC 20560, USA; Smithsonian Institution Press, London, England, UK.

GRAY, J. S., UGLAND, K. I. & LAMBSHEAD, J. 2004. On species accumulation and species-area curves. *Global Ecology and Biogeography,* 13**,** 567-568.

GREEN, J. L., HARTE, J. & OSTLING, A. 2003. Species richness, endemism and abundance patterns: tests of two fractal models in a serpentine grassland. *Ecology Letters,* 6**,** 919-928.

GREEN, J. L. & OSTLING, A. 2003. Endemics-area relationships: The influence of species dominance and spatial aggregation. *Ecology,* 84**,** 3090-3097.

HALLEY, J. M., SGARDELI, V. & TRIANTIS, K. A. 2014. Extinction debt and the species-area relationship: a neutral perspective. *Global Ecology and Biogeography,* 23**,** 113-123.

HANSKI, I., ZURITA, G. A., ISABEL BELLOCQ, M. & RYBICKI, J. 2013. Species-fragmented area relationship. *Proceedings of the National Academy of Sciences of the United States of America,* 110**,** 12715-12720.

HARDING, C. L. 2005. Wetland Inventory for the Fleurieu Peninsula, South Australia. Adelaide.

HARTE, J. 2000. *Scaling and self-similarity in species distributions: Implications for extinction, species richness, abundance, and range.*

HARTE, J., CONLISK, E., OSTLING, A., GREEN, J. L. & SMITH, A. B. 2005. A theory of spatial structure in ecological communities at multiple spatial scales. *Ecological Monographs,* 75**,** 179-197.

HARTE, J. & KINZIG, A. P. 1997. On the implications of species-area relationships for endemism, spatial turnover, and food web patterns. *Oikos,* 80**,** 417-427.

HE, F. & HUBBELL, S. P. 2011. Species-area relationships always overestimate extinction rates from habitat loss. *Nature,* 473**,** 368-71.

HE, F. L. & HUBBELL, S. 2013. Estimating extinction from species-area relationships: why the numbers do not add up. *Ecology,* 94**,** 1905-1912.

HE, F. L. & LEGENDRE, P. 2002. Species diversity patterns derived from species-area models. *Ecology,* 83**,** 1185-1198.

HEINO, J., VIRKKALA, R. & TOIVONEN, H. 2009. Climate change and freshwater biodiversity: detected patterns, future trends and adaptations in northern regions. *Biol Rev Camb Philos Soc,* 84**,** 39-54.

HEYWOOD, V. H., MACE, G. M., MAY, R. M. & STUART, S. N. 1994. Uncertainties in extinction rates. *Nature,* 368**,** 105-105.

HEYWOOD, V. H. & STUART, S. N. 1992. *Species extinctions in tropical forests,* London, Chapman & Hall.

HOULAHAN, J. E., KEDDY, P. A., MAKKAY, K. & FINDLAY, C. S. 2006. The effects of adjacent land use on wetland species richness and community composition. *Wetlands,* 26**,** 79-96.

JACKSON, S. T. & CHARLES, D. F. 1988. Aquatic macrophytes in Adirondack (New York) USA: lakes patterns of species composition in relation to environment. *Canadian Journal of Botany,* 66**,** 1449-1460.

JEFFRIES, M. 1991. The ecology and conservation value of forestry ponds in Scotland, United Kingdom. *Biological Conservation,* 58**,** 191-211.

JUNK, W. J. 2002. Long-term environmental trends and the future of tropical wetlands. *Environmental Conservation,* 29**,** 414-435.

KOH, L. P. & GHAZOUL, J. 2010. A matrix-calibrated species-area model for predicting biodiversity losses due to land-use change. *Conserv Biol,* 24**,** 994-1001.

KOH, L. P., LEE, T. M., SODHI, N. S. & GHAZOUL, J. 2010. An overhaul of the species-area approach for predicting biodiversity loss: incorporating matrix and edge effects. *Journal of Applied Ecology,* 47**,** 1063-1070.

KUUSSAARI, M., BOMMARCO, R., HEIKKINEN, R. K., HELM, A., KRAUSS, J., LINDBORG, R., OCKINGER, E., PARTEL, M., PINO, J., RODA, F., STEFANESCU, C., TEDER, T., ZOBEL, M. & STEFFAN-DEWENTER, I. 2009. Extinction debt: a challenge for biodiversity conservation. *Trends in Ecology & Evolution,* 24**,** 564-571.

LANG, P. & KRAEHENBUEHL, D. 1987. Plants of Particular Conservation Significance in South Australia's Agricultural Regions: Interim Report. Adelaide: Native Vegetation Management Branch, South Australian Department for Environment and Planning.

LAURANCE, W. F. 2008. Theory meets reality: How habitat fragmentation research has transcended island biogeographic theory. *Biological Conservation,* 141**,** 1731-1744.

LINTON, S. & GOULDER, R. 2000. Botanical conservation value related to origin and management of ponds. *Aquatic Conservation-Marine and Freshwater Ecosystems,* 10**,** 77-91.

MACARTHUR, R. & WILSON, E. 1967. *The theory of island biogeography,* Princeton, NJ, Princeton University Press.

MACROBERTS, B. R. & MACROBERTS, M. H. 1992. Floristics of four small bogs in western Louisiana with observations on species-area relationships. *Phytologia,* 73**,** 49-56.

MALCOLM, J. R., LIU, C. R., NEILSON, R. P., HANSEN, L. & HANNAH, L. 2006. Global warming and extinctions of endemic species from biodiversity hotspots. *Conservation Biology,* 20**,** 538-548.

MATTHEWS, J. W. 2003. Assessment of the floristic quality index for use in Illinois, USA, wetlands. *Natural Areas Journal,* 23**,** 53-60.

MAY, R. M., LAWTON, J. H. & STORK, N. E. 1995. *Assessing extinction rates*.

MOLLER, T. R. & RORDAM, C. P. 1985. Species numbers of vascular plants in relation to area, isolation and age of ponds in Denmark *Oikos,* 45**,** 8-16.

NEY-NIFLE, M. & MANGEL, M. 2000. Habitat loss and changes in the species-area relationship. *Conservation Biology,* 14**,** 893-898.

OERTLI, B., AUDERSET JOYE, D., CASTELLA, E., JUGE, R., CAMBIN, D. & LACHAVANNE, J. B. 2002. Does size matter? The relationship between pond area and biodiversity. *Biological Conservation,* 104**,** 59-70.

PANDIT, M. K., SODHI, N. S., KOH, L. P., BHASKAR, A. & BROOK, B. W. 2007. Unreported yet massive deforestation driving loss of endemic biodiversity in Indian Himalaya. *Biodiversity and Conservation,* 16**,** 153-163.

PEINTINGER, M., BERGAMINI, A. & SCHMID, B. 2003. Species-area relationships and nestedness of four taxonomic groups in fragmented wetlands. *Basic and Applied Ecology,* 4**,** 385-394.

PEREIRA, H. M., BORDA-DE-AGUA, L. & MARTINS, I. S. 2012. Geometry and scale in species-area relationships. *Nature,* 482**,** E3-4; author reply E5-6.

PEREIRA, H. M. & DAILY, G. C. 2006. Modeling biodiversity dynamics in countryside landscapes. *Ecology,* 87**,** 1877-1885.

PIMM, S. L. & ASKINS, R. A. 1995. Forest losses predict bird extinctions in eastern North America. *Proceedings of the National Academy of Sciences of the United States of America,* 92**,** 9343-9347.

PRESTON, F. W. 1962. Canonical distribution of commonness and rarity 1. *Ecology,* 43**,** 185-215.

REVENGA, C., CAMPBELL, I., ABELL, R., DE VILLIERS, P. & BRYER, M. 2005. Prospects for monitoring freshwater ecosystems towards the 2010 targets. *Philosophical Transactions of the Royal Society B-Biological Sciences,* 360**,** 397-413.

RICKETTS, T. H. 2001. The matrix matters: Effective isolation in fragmented landscapes. *American Naturalist,* 158**,** 87-99.

ROLON, A. S., LACERDA, T., MALTCHIK, L. & GUADAGNIN, D. L. 2008. Influence of area, habitat and water chemistry on richness and composition of macrophyte assemblages in southern Brazilian wetlands. *Journal of Vegetation Science,* 19**,** 221-228.

ROLON, A. S. & MALTCHIK, L. 2006. Environmental factors as predictors of aquatic macrophyte richness and composition in wetlands of southern Brazil. *Hydrobiologia,* 556**,** 221-231.

ROSSET, V., LEHMANN, A. & OERTLI, B. 2010. Warmer and richer? Predicting the impact of climate warming on species richness in small temperate waterbodies. *Global Change Biology,* 16**,** 2376-2387.

RYBICKI, J. & HANSKI, I. 2013. Species-area relationships and extinctions caused by habitat loss and fragmentation. *Ecology Letters,* 16**,** 27-38.

SCHOPF, T. J. M. 1974. Permo-Triassic extinctions - relation to sea-floor spreading. *Journal of Geology,* 82**,** 129-143.

SHI, J., MA, K., WANG, J., ZHAO, J. & HE, K. 2010. Vascular plant species richness on wetland remnants is determined by both area and habitat heterogeneity. *Biodiversity and Conservation,* 19**,** 1279-1295.

SIMBERLOFF, D. S. 1974. Permo-Triassic extinctions - effects of area on biotic equilibrium. *Journal of Geology,* 82**,** 267-274.

SMITH, A. B. 2010. Caution with curves: Caveats for using the species-area relationship in conservation. *Biological Conservation,* 143**,** 555-564.

SMITH, L. M. & HAUKOS, D. A. 2002. Floral diversity in relation to playa wetland area and watershed disturbance. *Conservation Biology,* 16**,** 964-974.

SODHI, N., BROOK, B. & BRADSHAW, C. 2009. Causes and consequences of species extinctions. *In:* LEVIN, S. E., CARPENTER, S., GODFRAY, H., KINZIG, A., LOREAU, M., LOSOS, J., WALKER, B., DS, W. & EDS.), A. (eds.) *The Princeton Guide to Ecology.* Princeton, New Jersey, USA: Princeton University Press.

STENDERA, S., ADRIAN, R., BONADA, N., CAÑEDO-ARGÜELLES, M., HUGUENY, B., JANUSCHKE, K., PLETTERBAUER, F. & HERING, D. 2012. Drivers and

stressors of freshwater biodiversity patterns across different ecosystems and scales: a review. *Hydrobiologia,* 696**,** 1-28.

STRAYER, D. L. & DUDGEON, D. 2010. Freshwater biodiversity conservation: recent progress and future challenges. *Journal of the North American Benthological Society,* 29**,** 344-358.

STRÖM, L., JANSSON, R. & NILSSON, C. 2012. Projected changes in plant species richness and extent of riparian vegetation belts as a result of climate-driven hydrological change along the Vindel River in Sweden. *Freshwater Biology,* 57**,** 49-60.

THOMAZ, S. M., SOUZA, D. C. & BINI, L. M. 2003. Species richness and beta diversity of aquatic macrophytes in a large subtropical reservoir (Itaipu Reservoir, Brazil): the influence of limnology and morphometry. *Hydrobiologia,* 505**,** 119-128.

TILMAN, D., MAY, R. M., LEHMAN, C. L. & NOWAK, M. A. 1994. Habitat destruction and extinction debt. *Nature,* 371**,** 65-66.

TRIANTIS, K. A., GUILHAUMON, F. & WHITTAKER, R. J. 2012. The island species-area relationship: biology and statistics. *Journal of Biogeography,* 39**,** 215-231.

TRIANTIS, K. A., MYLONAS, M., LIKA, K. & VARDINOYANNIS, K. 2003. A model for the species-area-habitat relationship. *Journal of Biogeography,* 30**,** 19-27.

ÚBEDA, B., DI GIACOMO, A. S., NEIFF, J. J., LOISELLE, S. A., POI, A. S. G., GALVEZ, J. A., CASCO, S. & COZAR, A. 2013. Potential Effects of Climate Change on the Water Level, Flora and Macro-fauna of a Large Neotropical Wetland. *Plos One,* 8.

UGLAND, K. I., GRAY, J. S. & ELLINGSEN, K. E. 2003. The species-accumulation curve and estimation of species richness. *Journal of Animal Ecology,* 72**,** 888-897.

ULRICH, W. 2005. Predicting species numbers using species-area and endemics-area relations. *Biodiversity and Conservation,* 14**,** 3351-3362.

VÖRÖSMARTY, C. J., MCINTYRE, P. B., GESSNER, M. O., DUDGEON, D., PRUSEVICH, A., GREEN, P., GLIDDEN, S., BUNN, S. E., SULLIVAN, C. A., LIERMANN, C. R. & DAVIES, P. M. 2010. Global threats to human water security and river biodiversity. *Nature,* 467**,** 555-561.

WEIHER, E. 1999. The combined effects of scale and productivity on species richness. *Journal of Ecology,* 87**,** 1005-1011.

WEIHER, E. & BOYLEN, C. W. 1994. Patterns and prediction of alpha and beta diversity of aquatic plants in adirondack (New York) lakes. *Canadian Journal of Botany,* 72**,** 1797-1804.

WILLIAMSON, L., HUDSON, M., O'CONNELL, M., DAVIDSON, N., YOUNG, R., AMANO, T. & SZEKELY, T. 2013. Areas of high diversity for the world's inland-breeding waterbirds. *Biodiversity and Conservation,* 22**,** 1501-1512.

WILSON, D. & PATON, D. C. 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.

ZEDLER, J. B. & KERCHER, S. 2005. Wetland resources: Status, trends, ecosystem services, and restorability. *Annual Review of Environment and Resources.*

Statement of authorship Chapter 2

Chapter 2   Diversity Patterns of Seasonal Wetland Plant Communities Mainly Driven by Rare Terrestrial Species

Abstract

In cleared landscapes, wetlands can represent important reservoirs of native plant diversity, which includes terrestrial species. Depending on study aims, non-wetland plants might be removed from analyses, affecting conclusions around biodiversity and community structure. I compared the native plant communities of seasonal wetlands in an agricultural landscape as defined geographically (including all species) with that of the obligate wetland assemblage. I was primarily concerned with determining how this design decision affects ecological and conservation conclusions. I analysed a survey database containing > 12,800 flora records from South Australia, selecting wetlands with near-complete censuses to remove sampling bias. I modelled occupancy, species-area relationships, β-diversity and nestedness under my contrasting community definitions. Terrestrial species were 52.4 % of total richness. Removing these species reduced wetland $\bar{\alpha}$-diversity by 41 %, but did not affect the scaling of richness with area (power-law species-area relationship $z = 0.25 \pm 0.01$). 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. Species nestedness including these rare terrestrial species was lower than predicted under null models, indicating rare species often do not co-occur with common species. The implication of this is a larger minimum wetland area must be maintained to conserve overall species diversity. While my survey database was suitable for this investigation, identifying adequate data was challenging and only a small proportion of records could be used.

Introduction

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 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. Soberon and Peterson, 2004, Hortal et al., 2007). It remains unclear to what extent these databases can contribute to modelling wetland biodiversity patterns or species extinction risk.

Wetlands, like all freshwater ecosystems, are susceptible to many stressors arising from global change (Houlahan et al., 2006, Davis et al., 2010, Dudgeon, 2010). 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 (Haukos and Smith, 1994, Brose, 2001, Kaeser and Kirkman, 2009). Even in highly urbanised or agricultural catchments, at least some wetland areas often remain and these can represent the only remaining areas of native vegetation (Haukos and Smith, 1994).

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. I 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*. I expected to find that terrestrial species are also an important component of these seasonal wetland plant communities, contributing to these intrinsic regional biodiversity conservation values.

Due to the much larger species pool for terrestrial – compared with wetland plants (Chambers et al., 2008) – I expected decreased compositional similarity and therefore higher β-diversity with the inclusion of terrestrial plants. The increased size of the species pool also suggests that individual terrestrial species would be found in fewer wetlands and thus their occupancies would be lower than for wetland plants. As the inclusion of terrestrial species also inevitably increases wetland $\bar{\alpha}$-diversity, I also expected to find higher intercepts and changes in the slopes of species-area relationships incorporating all surveyed species (Brose, 2001, Smith and Haukos, 2002). Hydrological heterogeneity is also a strong determinant of wetland plant richness and zonation (Grace and Wetzel, 1981,

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Brock and Casanova, 1997, Brose, 2001, Shi et al., 2010) and could reasonably be expected

to increase with size, so I anticipated the composition of smaller wetlands would be limited

in the wetland species they could support and represent a subset of larger sites. This would

be manifested as 'nesting' in wetland plant communities. I show that the terrestrial

component of these seasonal wetlands is not only diverse and highly variable, but that the

distribution of endemic species is less coincident with that of common species than null-

model expectations. This finding greatly increases the total area that is required to protect

the regional plant biodiversity as determined by seasonal wetlands in this heavily modified

landscape.

Methods

Study area

I selected a database 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 2.1; Fig. 2.1). 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 (~ 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.

Data

I used a comprehensive survey database (South Australian Wetland Inventory Database –
SAWID) compiled during a wetland mapping and data inventory project on the Fleurieu
Peninsula, South Australia (Harding, 2005). All available biological data collected over the
period 1977 to 2004 were incorporated within the database, which included a range of data
types collected across more than 20 projects. Three additional wetland vegetation surveys
done from 2005 to 2009 were also included. Effort was heavily weighted towards flora
surveys and so I focussed my analysis on vascular plants. Flora records included
opportunistic sightings (herbaria data), species lists based on non-quantitative 'meander'
surveys, and quadrat-based surveys. I matched all flora records from all surveys 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_Au
stralia) to ensure consistency across datasets. I also used the BDBSA to determine the
exotic status of plants and removed all non-native plants from further analysis (note that the
inclusion of exotic plants does not affect overall conclusions and Appendix 1).

Table 2.1 Regional database and analysis dataset summary statistics.

Region	rainfall range	500 - 800 m/yr
	maximum elevation	320 m
	central latitude	35.5 °S
Wetlands	total number	858
	median size	2.1 ha
	mean size	5.1 ha
	maximum size	167 ha
	total mapped wetland area	4280 ha
	wetlands with flora records	219
Full database records	total number of flora records	12812
	total flora species richness	715
	terrestrial species richness	410
	exotic terrestrial plant species	110 (27 %)
	rare or endangered terrestrial plant species	14 (3 %)
	total number of wetland flora records	9408
	total wetland species richness	305
	exotic wetland plant species	51 (17 %)
	rare or endangered wetland plant species	37 (12 %)
Analysis dataset	total wetlands	18
	median size	2.6 ha
	mean size	5.1 ha
	maximum size	34.7 ha
	mean richness (*all plants*) [95% CI]	39 [32.3, 45.0]
	mean richness (*wetland-only*) [95% CI]	23 [19.1, 27.3]
	β_1 all plants	0.26
	β_1 wetland-only	0.21
	total terrestrial species	146
	terrestrial exotics	58 (40 %)
	terrestrial rare species	1 (1 %)
	total *wetland-only* species	98
	wetland exotics	18 (18 %)
	wetland rare species	14 (11 %)

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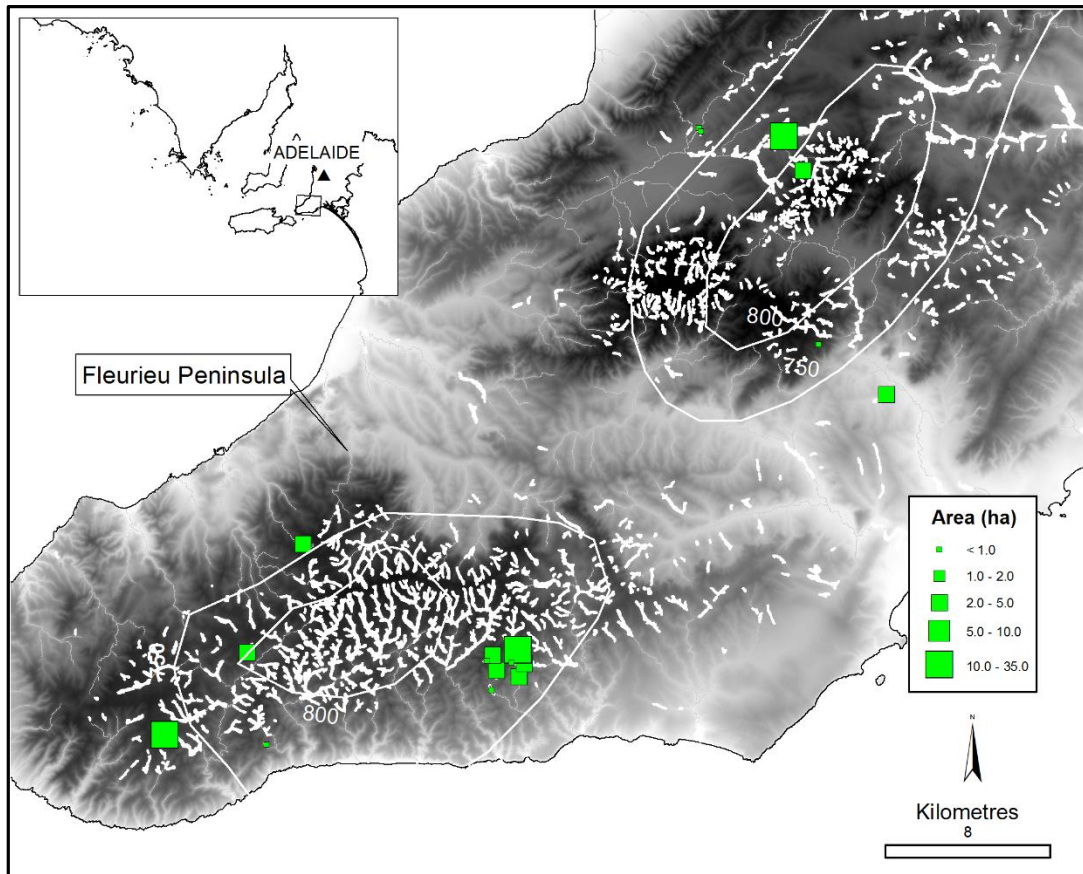
Figure 2.1 Fleurieu Peninsula, South Australia with wetland outlines shown in white. Squares denote the location of wetlands included in this study, where symbol size is coded by wetland area. Also shown are 750 and 800 mm isohyets and major watercourses. Shading represents elevation, with dark areas indicating higher areas that reach a maximum of ~ 320 m above sea level. Fleurieu wetlands occur mostly above elevations of around 250 m coinciding with mean annual rainfall > 750 mm. Wetland outlines are as defined based on a state agency spatial mapping program (Harding 2005).

Data pre-processing and subsetting

The database did not contain metadata on whether, or how, the completeness of sampling was established in wetland plant surveys. However, species richness was positively correlated with survey effort (measured as number of surveys), which is an indication of sampling bias. Following the general methods described in Hortal et al. (2007), I 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. To ensure meaningful

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comparisons, wetland surveys needed to have been done within a timeframe that is ecologically comparable. I used data from the most recent decade (2000 – 2009), during which time no widespread changes in land use have occurred. Records collected prior to 2000 represented around ~ 25% of records and were insufficient to support any comparison with wetlands during earlier decades.

Non-parametric species richness estimators (Colwell and Coddington, 1994) are used to predict the number of species missing from a sample. The fraction of observed to predicted species then provides a measure of the completeness of a species list and has been used to determine survey completeness in database records (Hortal et al., 2007, Lobo, 2008). I used the Chao 2 (Chao, 1987) estimator but found it was insufficient for correcting sampling bias (Appendix 1, Supporting Information). I instead used a three-step method to select full-census wetlands: (*i*) I initially filtered surveys to ensure good spatial interspersion, removing any wetlands where samples did not cover the main wetland dimensions; (*ii*) I ranked wetlands in descending order of the proportion of the total wetland area covered by sampling, selecting all wetlands above a threshold value to which I fit species-area curves. I decreased the sampled area threshold by adding wetlands until the slope value changed (at a threshold of < 0.25% of wetland area); (*iii*) I then tested the sensitivity of the selected wetlands to the Chao 2 predicted missing species, removing wetlands that were missing more than 25% of species, and ensuring slopes of a power-law species-area curve remained consistent. The selection method is described in detail in the following section.

Data adequacy, survey effort and wetland selection method

The 858 wetlands mapped in the Fleurieu Peninsula spatial database, SAWID (Harding, 2005) cover a total area of 4280 ha. Individual wetlands have a median and mean area of 2.1 and 5.1 ha, respectively (Table 2.1). The database contained a total of 12812 flora

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records of 715 different species, collected from 219 wetlands. The earliest record was collected in 1977 and the most recent in 2009. Although only comprising 23 % of total flora records, 57 % of recorded species were terrestrial plants (Table 2.1).

There were 165 wetlands with only a single survey (75 %), and 102 of these were collected using non-probabilistic survey methods during the 2005 inventory project (Harding, 2005). Four projects, collected data from 52 wetlands using a replicated, area-controlled survey method (6.1 % of total wetlands). Grain (sampling unit) size for these surveys ranged from 1 to 150 m^2, and mean sampling density varied from 0.9 to 14.1 samples ha^{-1}.

Prior authors have identified the need to remove bias from database records for biodiversity analysis (Hortal et al., 2007, Lobo, 2008). In this section I provide some additional information on my selection methods. I firstly separated opportunistic records from data collected using area-controlled (probabilistic) sampling methods, using the latter to choose wetlands with near-complete surveys. After selecting wetlands I included the opportunistic records to ensure maximum diversity was represented in analysis.

Database records date back to the late 1970s and I hoped to compare an earlier decade with the period 2000 – 2009, during which time climate has been consistent, though drier than earlier periods, and no major changes in land use have occurred. I firstly sub-divided the data into pre- and post-2000, but found too few records to make a meaningful comparison. Hence I limited analysis to the post-2000 data, which comprised around 75 % of flora records. To determine fully surveyed wetlands, I initially used the non-parametric, incidence-based species richness estimator 'Chao 2' (Chao, 1987), recommended for heterogeneous sampling units (Hortal et al., 2006), assessed sampling effort based on the number of predicted missing species. I included only wetlands with >80 % of predicted total richness.

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As observed in diverse seasonal wetlands in Georgia, USA, (Kaeser and Kirkman, 2009), rarefaction curves rarely reached asymptotes for my data, even in well-surveyed wetlands (Fig 2.2). This is likely a result of the diversity of habitats present in seasonal wetlands, which provide hydrological conditions ranging from terrestrial through to fully submersed. Surveys that sub-sample only a limited area of homogeneous hydrological conditions within a seasonal wetland are likely to appear complete based on rarefaction curves, and will have few missing species according to non-parametric species richness estimators. However, such sampling will probably underestimate diversity owing to incomplete coverage of the hydrological niche space meaning these are unreliable methods to determine the completeness of surveys.

On plotting the species-area relationship (Fig. 2.3), it was apparent that the Chao 2 method had not selected fully surveyed wetlands. This was a result of a number of surveys that were not properly interspersed across the wetland (see Fig 2.4). The clustering meant that only a limited range of hydrological conditions was sampled, adding to the spatial bias. Samples were assessed as being relatively complete by Chao 2 because of few singletons rather than being a comprehensive census of species.
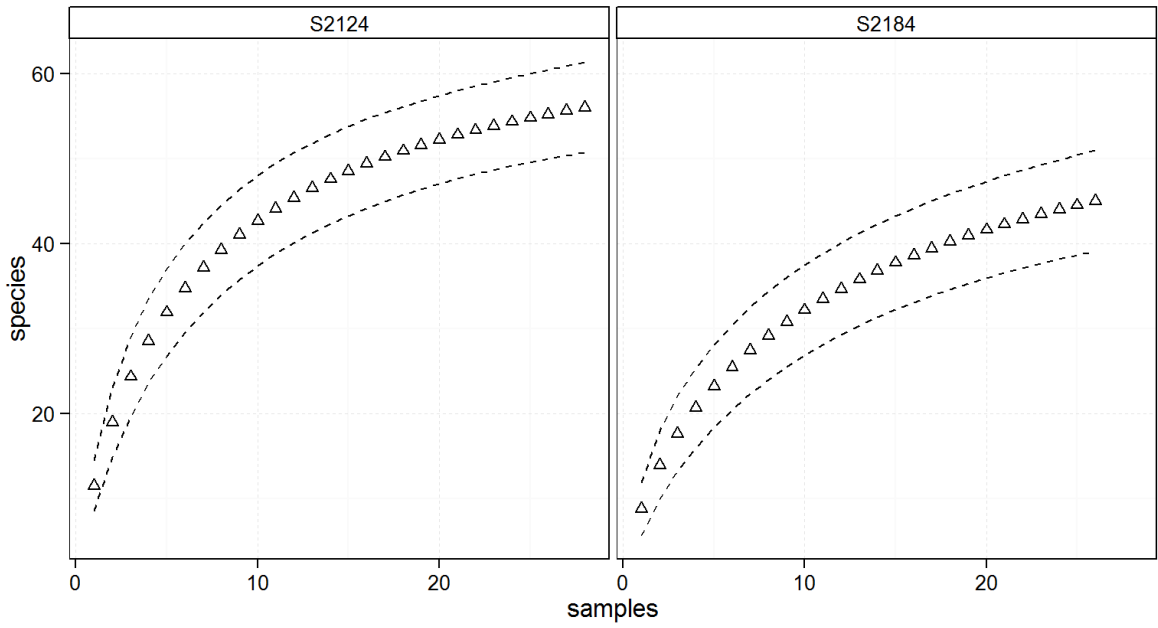
Figure 2.2 Example plot-based rarefaction curves for two wetlands that do not reach asymptote. These were among a number of wetlands exhaustively surveyed by me during 2008 and are known to be near-complete censuses. Triangles show the rarefied richness as each additional sample is added and the dotted lines show the 95 % confidence limits for this.
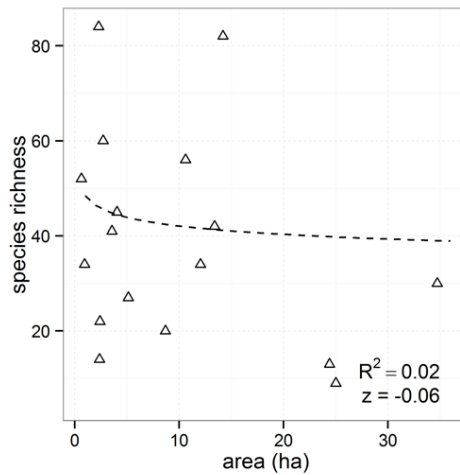
Figure 2.3 Species-area relationship for wetlands with near-complete census data selected according to the number of missing species using the Chao 2 non-parametric species richness estimate.

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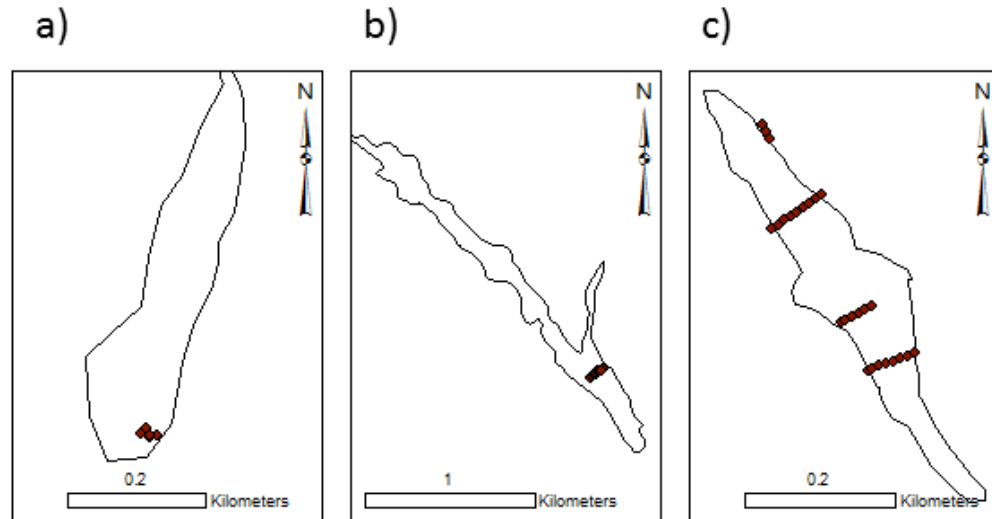
Figure 2.4 Examples of survey designs. Surveys from panels a) and b) were both selected by Chao 2 as having greater than 80 % of richness sampled, but they are poorly interspersed and unlikely to reflect diversity. Panel c) shows the characteristics of the spatial design that I considered would provide the best estimate of species richness with both longitudinal and transverse interspersion.

I instead used a three-step process to select wetlands with near-complete surveys. I first pre-filtered surveys manually, precluding surveys where sub-samples were clustered within small sections of the wetland (indicating a spatial bias – Fig. 2.4) rather than being well interspersed across the wetland area. This filtering included a subjective element as the first step to filter out poorly interspersed sampling was based only on visual inspection. Experience within these generally linear wetland systems, suggests hydrology – therefore, floral composition – changes both along and across the extent owing to fine-scale changes in hydrology such as the presence of localised springs. To ensure reasonable coverage of this within-site variability, I applied a general criterion requiring multiple samples to have been collected across the wetland short axis (transverse variation) in at least two locations along the long axis (longitudinal variation), dependent upon the wetland size. I precluded all wetlands not demonstrating this degree of interspersion.

I then ranked wetlands with suitable spatial sampling coverage in decreasing order according to the proportion of the total wetland area included in all sub-samples (range:

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0.004 – 14.3 %). I selected an initial group of wetlands based on the % wetland area sampled, starting with 2% and fit a power-function species-area relationship. I then decreased the size of the threshold, increasing the size of the group. With the addition of each new group of wetlands, I fit a new power curve, comparing it with the previous group. I stopped at a threshold (0.25 % of wetland area surveyed) where adding new wetlands changed the z parameter for the power-function species-area relationship to such a point that confidence intervals for the larger dataset fell outside that of the next smallest subset. I then tested the sensitivity of my selection method to the Chao 2 estimate, removing surveys estimated to be missing more than 25 % of species and re-fitting the power function SAR. Confidence intervals for the z parameter in the power function for the two datasets overlapped and I concluded that no bias was introduced by including samples with poor completeness according to the Chao 2 method.

I note that even among those samples with good spatial design and replication, rarefaction curves generally did not asymptote. Survey experience in Fleurieu wetlands suggests that only species-poor wetlands impacted by heavy grazing disturbance or impacted by water extraction tend to reach a clear asymptote. I recognise that using the observed species-area relationship to determine complete surveys could result in the loss of legitimate surveys from wetlands of unusually high or low diversity. In this case I saw no alternative to using area-scaling relationships because size differences among wetlands made it impossible to use established methods that rely on the number of survey records in regular-sized grids (e.g., Hortal et al. 2007; Lobo 2008). Given the strength of the species-area relationship in my baseline dataset, and the consistency of parameter estimates in my predictive model with published values, I believe that my analysis dataset provides a reliable statistical sample of these wetland plant communities.

Plant functional groups

I used the plant functional group assignments of Casanova and Brock (2000) to distinguish obligate wetland plants from those capable of persisting within the terrestrial landscape matrix. I based my assignment into functional groups on Casanova (2011) and the opinion of local aquatic botanists (*pers. comm.* J. Nicol, South Australian Research and Development Institute). I 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). My final two wetland-community datasets comprised *all plants* and *wetland-only* taxonomic subsets of the native vegetation.

Analysis

I analysed three statistical models for each dataset: (*i*) species occupancy, (*ii*) species-area relationships and (*iii*) distance-decay in community similarity – an expression of species turnover or β-diversity (Anderson et al., 2011). To distinguish competing occupancy frequency distributions, I 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 freshwater ecosystems that I

reviewed (Tables 1.1 and 1.2). I fitted log-log transformed power function species-area

models to each dataset to test whether the value of the *z* parameter (slope) and variance

explained (R^2) differed between *wetland-only* and *all plants* communities.

β-diversity (Whittaker, 1960) describes changes in community composition, or

differentiation along an environmental gradient and has been described using many

different measures. To compare this value for my study with previously published wetland

data, I 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 is total observed species

richness; $\bar{\alpha}$ is mean wetland species richness; N is the number of wetlands; and, β_1 can be

interpreted as the average compositional turnover between wetlands (range: 0 to 1)

(Harrison et al., 1992). I 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 (Tables 4 and 5).

Table 2.2 published wetland and aquatic ecosystem species richness data and calculated
beta-1 (β1) index of (Harrison et al., 1992). Studies above the line are on deeper water
systems, while those below the line were of shallow water, similar to study wetlands.

source	γ-div	ᾱ	n	β_1	wetland type	country
Thomaz et al. (2003)	35	17	8	0.15	lakes	Brazil
Akasaka et al. (2010)	49	3.8	55	0.22	lakes	Japan
Capers et al. (2009)	82	11.3	99	0.06	lakes	USA
Chappuis et al. (2012)	314	137	41	0.03	mixed	Multiple
Friday (1987)	31	7.94	16	0.19	ponds	England
Jeffries (1991)	94	12.6	42	0.16	ponds	Scotland
Jackson and Charles (1988)	78	13.2	31	0.16	lakes	US
Linton and Goulder (2003)	70	10.1	57	0.11	ponds	UK
Oertli et al. (2002)	153	11.6	80	0.15	ponds	Swis
Rolon et al. (2012)	31	11	16	0.12	ponds	Brazil
Ebert and Balko (1987)	29	14.4	46	0.02	temp ponds	US

source	γ-div	ᾱ	n	β₁	wetland type	country
Nicolet et al. (2004)	181	17	71	0.14	temp ponds	UK
Rey Benayas et al. (1999)	237	23.6	66	0.14	sedge meadow	Spain
Matthews (2004)	312	31.4	56	0.16	sedge meadow	US
Rolon et al. (2008)	105	28.9	15	0.19	wetlands	Brazil
Rolon and Maltchik (2006)	153	8.7	126	0.13	wetlands	Brazil
Shi et al. (2010)	266	58	51	0.07	wetlands	China
Houlahan et al. (2006)	691	159	58	0.06	wetlands	Canada
Boughton et al. (2010)	128	22.5	60	0.08	wetlands	US
Peintinger et al. (2003)	316	105	36	0.06	fens	Swiss
Duval et al. (2012)	103	53	4	0.31	fens	Canada
Brose (2001) wetland plants	52	9	58	0.08	wetlands	Germany
Murray-Hudson et al. (2012)	390	31	74	0.16	marshes	US
Pollock et al. (1998)	233	52	16	0.23	wetland	US
De Steven and Toner (2004)	300	22	57	0.23	wetlands	US
Kaeser and Kirkman (2009)	378	169	9	0.16	wetlands	US

Table 2.3 Mean and confidence intervals for shallow and deep water inland aquatic ecosystems.

wetland type	mean β_1 [95 % CI]
shallow water	0.15 [0.108, 0.186]
deep water	0.13 [0.092, 0.162]
all aquatic systems	0.14 [0.111, 0.164]

Distance-decay of similarity is also an expression 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 (Soininen et al., 2007, Anderson et al., 2011), here represented by my two wetland plant communities. I 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: $S = S_0e^{-cd}$, where S is similarity at

distance d, S_0 is the maximum similarity between two sites, and c is a fitting parameter.

Linear and log-linear models are also commonly applied functions (Soininen et al., 2007),

but the distribution of the data suggested a functional form with a more rapid initial decay. I

therefore fit a power function: $S = ad^{-b}$, where S and d take their above values, and a and b

are fitted model parameters. I compared model support for the power, negative exponential,

linear and log-linear distance-decay functions using Akaike's information criterion. I

compared the parameter values for the top-ranked model for both communities. I 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. I did all modelling using the R platform (R Core Team, 2014).

Ranked species occupancy curves are based on marginal totals and provide only

limited insights of community patterns; I therefore also calculated nestedness within the

two communities (Hui, 2012). I 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. I 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 latter representing

perfect nestedness. I 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,

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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 $Z = [x\text{-}\mu]/\sigma$ 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 to 10; median = 1) was positively correlated with species richness (Spearman rank correlation $\rho_s = 0.41$, $n = 219$, $p < 0.001$). My sampling assessment method identified 18 wetlands with survey data representing near-complete censuses. This represents 2 % of the total mapped wetland number and 8% of the wetlands within the database with flora records. Native species richness recorded for the overall database was 554 species, 300 terrestrial and 254 wetland species; 3 % of terrestrial and 12 % of species recorded in wetlands are listed under South Australian *National Parks and Wildlife Act 1972* as having a status of rare or endangered (Table 2.1). For the analysis datasets *all plants* and *wetland-only*, values for total native species richness were 168 and 80, respectively (see Table 2.1). Proportionally, there were more than twice as many terrestrial species that were classed as 'exotic' compared to wetland species (40 vs. 18 %), and 11 % of *wetland-onl*y species were rare compared with only a single rare terrestrial species (Table 2.1). At the wetland scale, including terrestrial native plants increased mean species richness from (mean [± 95% confidence limits] = 23 [19.1, 27.3]) to 39 [32.3, 45.0] (Table 2.1).

The median percentage of total wetland area sampled per survey was 0.16%, and the maximum was 14.3%. Total wetland area sampled was negatively correlated with wetland area over all area-controlled surveys (Spearman rank correlation $\rho_s = -0.71$, $n = 52$, $p <$

0.001), but not for the subset of near-complete census wetlands ($\rho_s = -0.23$, $n = 18$, $p = 0.34$). Compared with the full wetland size distribution, the median size of full-census wetlands was larger (2.6 vs. 2.1 ha), but mean size was the same (5.1 ha).

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. 2.5). 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. 2.6; Table 2.4). The AIC weight (wAIC ≈ parameter-corrected relative model probability) exceeded 0.99 for both models. The coefficient of determination for regression model fits were both > 0.99 (Fig. 2.6). The occupancy frequency distribution for *all plants* was strongly unimodal and dominated by infrequently observed (satellite) species (Fig 2.5) for *all plants*, but this mode was reduced for *wetland-only* plants, which approached bimodality with an increase in frequently observed (core) species. The difference between the two occupancy distributions in Figure 2.5 represents the occupancies for terrestrial-only species and highlights the dominance of species with a small area of occupancy. The mean area of occupancy for *terrestrial* species was 20.3 ha, a little of half that of *wetland-only* plants (38.9 ha).
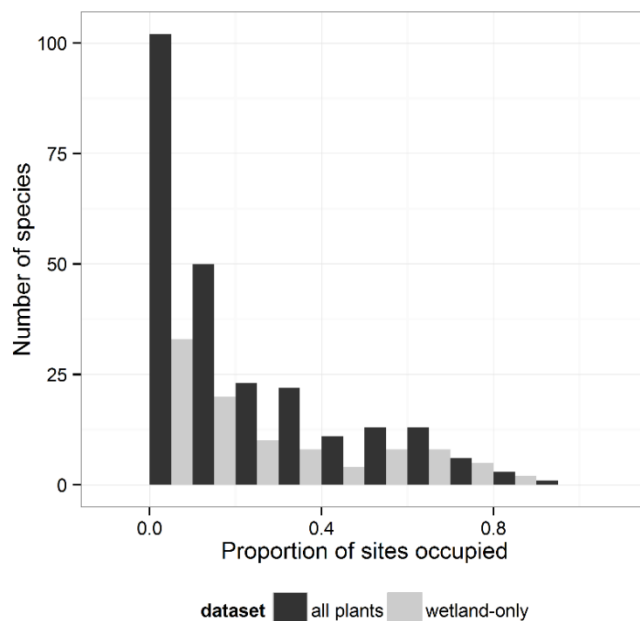
Figure 2.5 Comparison of binned species occupancy data for native plants (All species $n = 168$ species and wetland-only $n = 80$ species). Shown are the proportion of 18 wetlands where each species was observed (*x*-axis) and the number of species within each bin (*y*-axis). The difference in height between the black and grey bars indicates the contribution of terrestrial plants - note the extreme dominance of the infrequently occurring (< 10 % of sites) rare ('satellite') species.
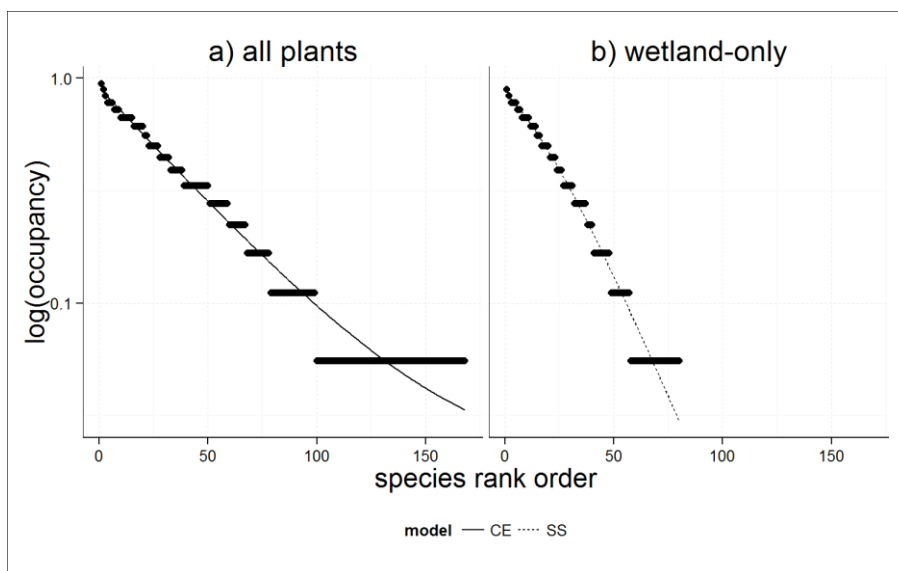
Figure 2.6 Ranked species-occupancy curves for (a) *all plants* and (b) *wetland-only* datasets. The *x*-axis shows the rank order of each species (highest occupancy is ranked 1st). The top-ranked model is also shown, along with the coefficient of determination for each fit. CE = concave exponential function; SS = symmetric sigmoidal (see Jenkins 2011).

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The power function species-area relationship had good support for both the *all plants* and *wetland-only* datasets, the fit being marginally better when terrestrial plants were included ($R^2 = 0.71$ vs 0.68; Fig. 2.7, Table 2.4). Slopes (z) were similar for the two datasets (*all plants*: 0.24; *wetland-only*: 0.26) with overlapping confidence intervals (Table 2.4). My slopes did not differ, but were slightly high compared with 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 1.2).
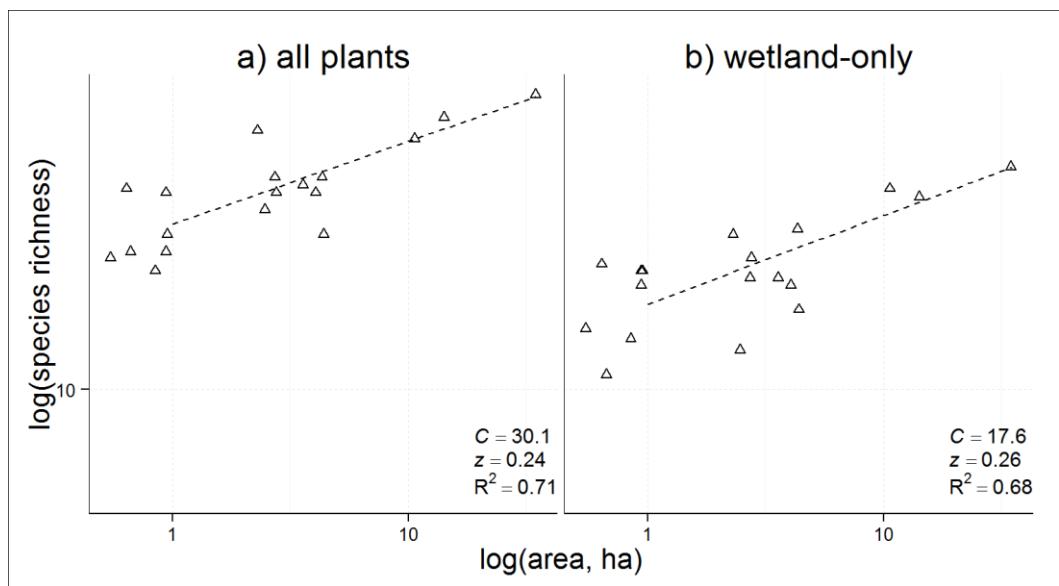
Figure 2.7 Species-area relationships for *all plants* (a) and *wetland-only* (b) datasets. The log-log implementation of the power-law species-area model is fitted to each data subset and the value for the intercept (C) slope parameter (z) and coefficient of determination (R^2) are shown in the bottom right of each panel.

Table 2.4 Model coefficients and goodness of fit for three ecological patterns for *all plants* and *wetland-only* datasets. Ranked species occupancy curves: Akaike's information criterion weights (*w*AIC) for the top-ranked models. Species-area relationships: power-law model coefficients and 95% confidence intervals are shown along with model goodness of fit (R^2) (see also Fig. 2.7). Distance decay in similarity: Species turnover in wetland plant community composition as a function of inter-wetland distance. Shown are model coefficients with 95% confidence intervals, *w*AIC and R^2 for the top-ranked power-law model (see also Fig. 2.8).

Pattern	Model	Statistic	All-plants	Wetland-only
Ranked species occupancy curve[a]	Symmetrical sigmoidal	*w*AIC	-	> 0.99
	Concave exponential	*w*AIC	> 0.99	-
Species-area relationship	Power-law	c	30.2 [25.1, 35.4]	17.6 [14.6, 20.8]
		z	0.23 [0.12, 0.35]	0.26 [0.17, 0.34]
		R^2	0.71	0.69
Distance-decay in similarity[a]	Power-law	a	0.43 [0.40, 0.46]	0.46 [0.43, 0.50]
		b	-0.22 [-0.26,-0.19]	-0.19 [-0.22, -0.16]
		*w*AIC	> 0.99	> 0.99
		R^2	0.52	0.40

[a] results for top-ranked model shown only - see Table 2.5 for support for all models and Jenkins (2011) and Hui (2012) for RSOC model formulae

Table 2.5 model selection table for the ranked species occupancy curves fitted. Model structures are described in Jenkins (2011) and Hui (2012).

regression model	all plants			wetland-only		
	AIC	ΔAIC	*w*AIC	AIC	ΔAIC	*w*AIC
exponential concave	-812.9	-	0.99	-375.9	30.2	0
exponential convex	-274.1	538.8	0	-168.7	237.4	0
lognormal	39.6	852.4	0	-49.4	356.7	0
symmetric sigmoidal	-794.0	18.9	0	-406.1	-	1.0
asymmetric sigmoidal	-242.4	570.5	0	-91.2	314.9	0
linear	-278.9	533.9	0	-172.9	233.2	0
power exponential	-802.3	10.5	0.01	-373.8	32.3	0

Average compositional turnover was higher in the *all plants* dataset ($\beta_1 = 0.26$) than the *wetland-only* dataset ($\beta_1 = 0.21$) (Table 2.4). These values were both high compared with the distribution of β_1 estimated from previously published studies, exceeding the upper confidence limit (mean [$\pm$ 95% confidence limits] = 0.15 [0.11, 0.19], $n = 14$; Tables 2.2 and 2.3). The lower species turnover between *wetland-only* communities resulted in a slightly higher (less negative) estimate for the slope (*b*) parameter of the distance-decay relationship (-0.19 vs. -0.22 for *wetland-only* and *all plants* respectively), but confidence intervals for both communities overlapped (Fig 2.8, Table 2.4) and the top-ranked model was the power-law in both cases (Table 2.6). *Wetland-only* community similarity was also more variable as shown by the lower variance explained (R^2 *all plants* = 0.50, *wetland-only* = 0.40). Wetlands with the most similar community composition tended to be located within the same catchment (Fig 2.8), although dissimilar wetlands were also present.
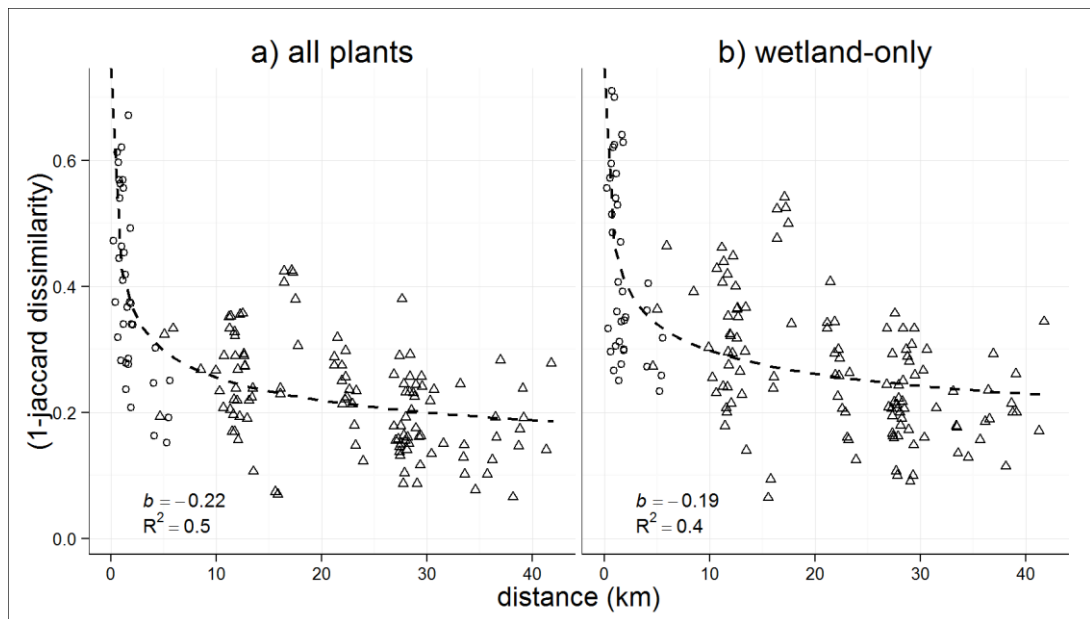
Figure 2.8 Species turnover as a function of geographical distance (distance-decay) for wetlands in the same catchment (open circles) or different catchments (open triangles), modelled with a power function. The *y*-axis indicates the similarity in species composition between wetlands (measured as 1-Jaccard dissimilarity index), with higher values indicating more similar wetland communities.

Table 2.6 model selection table for the distance-decay models

model	all plants			wetland-only		
	AIC	ΔAIC	*w*AIC	AIC	ΔAIC	wAIC
power law	-308.8	-	1.00E+00	-255.8	-	1.00E+00
negative exponential	-143.1	165.7	1.06E-36	-125.5	130.3	5.00E-29
linear	134.8	443.6	4.81E-97	127.8	383.6	5.11E-84
log-linear	125.6	434.4	4.64E-95	128.1	383.9	4.29E-84

Total nestedness did not differ from null-model expectations for *wetland-only* community composition (sites) or occupancies (species), but was lower than expected for *all plants*, providing evidence for anti-nestedness in the *all plants* dataset (Table 2.7). This was largely driven by patterns of species occupancies (*all plants Z* = -2.2, *p* = 0.016), with little support for evidence of anti-nesting in community composition among sites (*all plants Z* = -1.4, *p* = 0.081).

Table 2.7 Nestedness analysis for the two datasets based on overlap and decreasing fill metrics (NODF). 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 value for *all plants* was 0.23, and for wetland –only plants was 0.29.

Dataset	NODF[a]	Estimate[b]	Expected[c]	Z	P_Z
all plants	total	34.9	39.1	-2.15	0.016
	sites	49.2	51.9	-1.40	0.081
	species	34.8	39.0	-2.15	0.016
wetland-only	total	47.5	50.5	-1.07	0.142
	sites	57.1	58.5	-0.54	0.295
	species	47.1	50.1	-1.08	0.140

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 & Ulrich 2011).

Discussion

Terrestrial species were a large and important component of total plant biodiversity, representing more than half of the species present in my dataset. The inclusion of terrestrial species changed occupancy distributions to a strongly unimodal pattern dominated by rare (satellite) species. This suggests that wetland fringes offer habitats for many rare species in the wetland systems which were not found alongside common species. The inclusion of these rare terrestrial plants increased species turnover as indeed shown by my analyses (Table 2.4). To ensure that all species currently found in wetlands persist in the landscape, a large proportion of the existing wetland area would need to be conserved.

I 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 bimodal in shape apparent in occupancy curves as well as histograms of the data (Fig 2.5). 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 (Jenkins, 2011, Hui, 2012). Jenkins (2011) proposed different causal mechanisms for the two models, with dispersal limitation or high disturbance leading to an exponential concave model and habitat heterogeneity and moderate disturbance resulting in sigmoidal patterns. While the idea that disturbance dominates the distribution of terrestrial (largely wetland-fringe) plants accords with my expectation, several authors have suggested occupancy distributions are not reliable indicators of biological mechanisms and patterns can be scale-dependent (Brown, 1984, McGeoch and Gaston, 2002, Hui, 2012).

I hypothesised that reliance on hydrological niches would create nested patterns in *wetland-only* communities, but found no evidence of this – *wetland-only* site-based species patterns did not differ from null-model expectations. This suggests that wetland species are probably randomly distributed across wetland habitats. In contrast, when terrestrial species were included in the analysis, I found good evidence that species occupancy patterns were anti-nested. Anti-nestedness for species occupancies tends to occur when endemic species (those with a limited spatial distribution) are not found at those sites where widespread species occur (Almeida-Neto et al., 2008). This pattern partly arose because a high number 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 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). High nestedness has been found previously for sedge meadows in Illinois, USA (Matthews, 2004), but Matthews et al. (2015) found that anti-nestedness was more frequently observed in habitat islands, which includes wetlands, suggesting earlier work might be unreliable because of the metrics and null models adopted.

Observed power-law behaviour ($z \sim 0.25$) for my wetland species was typical for habitat isolates such as islands (Rosenzweig, 1995, Drakare et al., 2006, Triantis et al., 2012), but above average when compared to other wetland systems. The variance explained by the species-area model was ≈ 0.7 for both datasets. The similarity in z parameter estimates and the variance explained are slightly at odds with prior studies separating terrestrial and wetland plants in seasonal wetlands. Both Brose (2001) and Smith and Haukos (2002) found 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 in space than wetland plants. However, neither of the prior studies

explained more than 25% of overall variation, and 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 east German wetlands (Brose, 2001) could have increased environmental variability. The many wetlands and lower overall species richness in those studies might also have contributed because these can decrease R^2 in the log-log implementation of the power-law (Triantis et al., 2012).

Species turnover was, as I anticipated, lower for *wetland-only* plant communities, but high in both communities compared to previously published results (Tables 2.1 and 2.2). Slopes of distance-decay models did not differ, but compositional similarity for both communities was higher for wetlands within a catchment, although this decayed rapidly with distance. Fleurieu wetlands are almost invariably associated with watercourses (Fig. 2.1), and high 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 invasive species spread and can make wetlands more susceptible to climate change through its effects on streamflow patterns (Nilsson et al., 2010).

I found that removing sampling bias for wetland databases presents a different challenge than for relatively homogeneous habitat types because of the internal hydrological gradients present (Appendix 1, Supporting Information). Hydrological heterogeneity is positively correlated with plant species richness in wetlands (e.g. Brose, 2001, Shi et al., 2010) and is an important determinant of wetland plant zonation (Grace and Wetzel, 1981, Brock and Casanova, 1997, Casanova and Brock, 2000). The inability to ensure full coverage of the hydrological gradient might preclude the use of some data sources for the types of analysis I have presented here, because it would be impossible to determine sampling adequacy and completeness (Appendix 1, Supporting Information).

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.

Within the highly modified Fleurieu Peninsula landscape, wetlands are recognised as important habitats for terrestrial native fauna, most notably the endangered *Stipiturus malachurus intermedius* (southern emu wren) (Wilson and Paton, 2004). More than 15 % of *wetland-only* and 3 % of terrestrial plant species recorded in the full database were either rare, endangered or vulnerable and therefore of conservation importance. Around 6700 ha (~ 5.5 % of the region) is held in conservation reserves. There are 16 wetlands (total area of 67.3 ha) included within these reserves, representing 1.9 % of the total number of wetlands by number and 1.6 % by area. While populations of many of the rare species occuring in Fleurieu wetlands might also be present within formal conservation reserves, the data to determine what proportion of species this represents were not available. Given their rare status, it seems unlikely that they would be present in large populations. As Fleurieu wetlands are widely distributed across the landscape the additional populations of all native species they support are clearly important for regional plant conservation.

My analysis indicates that Fleurieu wetland plant communities are diverse and variable in their composition by global standards, and occupancy is dominated by infrequently occurring terrestrial species that contribute much of the diversity and variability in community composition. By focussing on the different diversity characteristics of richness, occupancy, nestedness and turnover I provide a more complete picture of how these facultative wetland species affect overall biodiversity. Although I obtained these estimates of wetland biodiversity using an existing survey database, only 8% of wetlands with flora records were suitable for analysis; I therefore recommend that more

wetland databases be critically evaluated before they can be used to address issues of future

wetland biodiversity trends.

References

AKASAKA, M., TAKAMURA, N., MITSUHASHI, H. & KADONO, Y. 2010. Effects of land use on aquatic macrophyte diversity and water quality of ponds. *Freshwater Biology,* 55**,** 909-922.

ALMEIDA-NETO, M., GUIMARAES, P., GUIMARAES, P. R., LOYOLA, R. D. & ULRICH, W. 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos,* 117**,** 1227-1239.

ALMEIDA-NETO, M. & ULRICH, W. 2011. A straightforward computational approach for measuring nestedness using quantitative matrices. *Environmental Modelling & Software,* 26**,** 173-178.

ANDERSON, M. J., CRIST, T. O., CHASE, J. M., VELLEND, M., INOUYE, B. D., FREESTONE, A. L., SANDERS, N. J., CORNELL, H. V., COMITA, L. S., DAVIES, K. F., HARRISON, S. P., KRAFT, N. J. B., STEGEN, J. C. & SWENSON, N. G. 2011. Navigating the multiple meanings of beta diversity: a roadmap for the practicing ecologist. *Ecology Letters,* 14**,** 19-28.

ARRHENIUS, O. 1921. Species and area. *Journal of Ecology,* 9**,** 95-99.

BALIAN, E. V., SEGERS, H., LEVEQUE, C. & MARTENS, K. 2008. The freshwater animal diversity assessment: An overview of the results. *Hydrobiologia,* 595**,** 627-637.

BOUGHTON, E. H., QUINTANA-ASCENCIO, P. F., BOHLEN, P. J., JENKINS, D. G. & PICKERT, R. 2010. Land-use and isolation interact to affect wetland plant assemblages. *Ecography.*

BROCK, M. A. & CASANOVA, M. T. 1997. Plant life at the edges of wetlands: ecological responses to wetting and drying patterns. *In:* KLOMP, N., LUNT, I. (ed.) *Frontiers in Ecology: Building the Links.* Oxford: Elsevier.

67

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.

BROWN, J. H. 1984. On the relationship between abundance and distribution of species. *American Naturalist,* 124**,** 255-279.

BURNHAM, K. & ANDERSON, D. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach,* New York, Springer.

CAPERS, R. S., SELSKY, R., BUGBEE, G. J. & WHITE, J. C. 2009. Species richness of both native and invasive aquatic plants influenced by environmental conditions and human activity. *Botany-Botanique,* 87**,** 306-314.

CASANOVA, M. T. 2011. Using water plant functional groups to investigate environmental water requirements. *Freshwater Biology,* 56**,** 2637-2652.

CASANOVA, M. T. & BROCK, M. A. 2000. How do depth, duration and frequency of flooding influence the establishment of wetland plant communities? *Plant Ecology,* 147**,** 237-250.

CHAMBERS, P. A., LACOUL, P., MURPHY, K. J. & THOMAZ, S. M. 2008. Global diversity of aquatic macrophytes in freshwater. *Hydrobiologia,* 595**,** 9-26.

CHAO, A. 1987. Estimating the population-size for capture recapture data with unequal catchability. *Biometrics,* 43**,** 783-791.

CHAPPUIS, E., BALLESTEROS, E. & GACIA, E. 2012. Distribution and richness of aquatic plants across Europe and Mediterranean countries: patterns, environmental driving factors and comparison with total plant richness. *Journal of Vegetation Science,* 23**,** 985-997.

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.

COLWELL, R. K. & CODDINGTON, J. A. 1994. Estimating terrestrial biodiversity

    through extrapolation. *Philosophical Transactions of the Royal Society of London*

    Series B-Biological Sciences, 345**,** 101-118.

DAVIS, J., SIM, L. & CHAMBERS, J. 2010. Multiple stressors and regime shifts in

    shallow aquatic ecosystems in antipodean landscapes. *Freshwater Biology,* 55**,** 5-18.

DE STEVEN, D. & TONER, M. M. 2004. Vegetation of upper coastal plain depression

    wetlands: Environmental templates and wetland dynamics within a landscape

    framework. *Wetlands,* 24**,** 23-42.

DRAKARE, S., LENNON, J. J. & HILLEBRAND, H. 2006. The imprint of the

    geographical, evolutionary and ecological context on species-area relationships.

    Ecol Lett, 9**,** 215-27.

DUDGEON, D. 2010. Prospects for sustaining freshwater biodiversity in the 21st century:

    linking ecosystem structure and function. *Current Opinion in Environmental*

    Sustainability, 2**,** 422-430.

DUFFIELD, R., T., M., M., R. & B., H. 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*. Adelaide:

    Conservation Council of South Australia and the Nature Conservation Society of

    South Australia.

DUVAL, T. P., WADDINGTON, J. M. & BRANFIREUN, B. A. 2012. Hydrological and

    biogeochemical controls on plant species distribution within calcareous fens.

    Ecohydrology, 5**,** 73-89.

69

EBERT, T. A. & BALKO, M. L. 1987. Temporary pools as islands in space and in time - the biota of vernal pools in San Diego, southern California, USA. *Archiv Fur Hydrobiologie,* 110**,** 101-123.

ELITH, J., GRAHAM, C. H., ANDERSON, R. P., DUDIK, M., FERRIER, S., GUISAN, A., HIJMANS, R. J., HUETTMANN, F., LEATHWICK, J. R., LEHMANN, A., LI, J., LOHMANN, L. G., LOISELLE, B. A., MANION, G., MORITZ, C., NAKAMURA, M., NAKAZAWA, Y., OVERTON, J. M., PETERSON, A. T., PHILLIPS, S. J., RICHARDSON, K., SCACHETTI-PEREIRA, R., SCHAPIRE, R. E., SOBERON, J., WILLIAMS, S., WISZ, M. S. & ZIMMERMANN, N. E. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography,* 29**,** 129-151.

FAUTH, J. E., BERNARDO, J., CAMARA, M., RESETARITS, W. J., VANBUSKIRK, J. & MCCOLLUM, S. A. 1996. Simplifying the jargon of community ecology: A conceptual approach. *American Naturalist,* 147**,** 282-286.

FORDHAM, D. A., AKCAKAYA, H. R., ARAUJO, M. B., ELITH, J., KEITH, D. A., PEARSON, R., AULD, T. D., MELLIN, C., MORGAN, J. W., REGAN, T. J., TOZER, M., WATTS, M. J., WHITE, M., WINTLE, B. A., YATES, C. & BROOK, B. W. 2012. Plant extinction risk under climate change: are forecast range shifts alone a good indicator of species vulnerability to global warming? *Global Change Biology,* 18**,** 1357-1371.

FRIDAY, L. E. 1987. The diversity of macroinvertebrate and macrophytes communities in ponds. *Freshwater Biology,* 18**,** 87-104.

GRACE, J. B. & WETZEL, R. G. 1981. Habitat partitioning and competitive displacement in cattails (Typha) - experimental field studies. *American Naturalist,* 118**,** 463-474.

GRAHAM, C. H., FERRIER, S., HUETTMAN, F., MORITZ, C. & PETERSON, A. T. 2004. New developments in museum-based informatics and applications in biodiversity analysis. *Trends in Ecology & Evolution,* 19**,** 497-503.

HARDING, C. L. 2005. Wetland Inventory for the Fleurieu Peninsula, South Australia. Adelaide.

HARRISON, S., ROSS, S. J. & LAWTON, J. H. 1992. Beta-diversity on geographic gradients in Britain. *Journal of Animal Ecology,* 61**,** 151-158.

HAUKOS, D. A. & SMITH, L. M. 1994. The importance of playa wetlands to biodiversity of the Southern High Plains. *Landscape and Urban Planning,* 28**,** 83-98.

HOLLAND, C. C., HONEA, J. E., GWIN, S. E. & KENTULA, M. E. 1995. Wetland degradation and loss in the rapidly urbanizing area of Portland, Oregon. *Wetlands,* 15**,** 336-345.

HORTAL, J., BORGES, P. A. V. & GASPAR, C. 2006. Evaluating the performance of species richness estimators: sensitivity to sample grain size. *Journal of Animal Ecology,* 75**,** 274-287.

HORTAL, J., LOBO, J. M. & JIMENEZ-VALVERDE, A. 2007. Limitations of biodiversity databases: Case study on seed-plant diversity in Tenerife, Canary Islands. *Conservation Biology,* 21**,** 853-863.

HOULAHAN, J. E., KEDDY, P. A., MAKKAY, K. & FINDLAY, C. S. 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 Ecology,* 13**,** 30-35.

JACKSON, S. T. & CHARLES, D. F. 1988. Aquatic macrophytes in Adirondack (New York) USA: lakes patterns of species composition in relation to environment. *Canadian Journal of Botany,* 66**,** 1449-1460.

JEFFRIES, M. 1991. The ecology and conservation value of forestry ponds in Scotland, United Kingdom. *Biological Conservation,* 58**,** 191-211.

JENKINS, D. G. 2011. Ranked species occupancy curves reveal common patterns among diverse metacommunities. *Global Ecology and Biogeography,* 20**,** 486-497.

KAESER, M. J. & KIRKMAN, L. K. 2009. Estimating total plant species richness in depressional wetlands in the Longleaf Pine ecosystem. *Wetlands,* 29**,** 866-874.

LINTON, S. & GOULDER, R. 2003. Species richness of aquatic macrophytes in ponds related to number of species in neighbouring water bodies. *Archiv Fur Hydrobiologie,* 157**,** 555-565.

LOBO, J. M. 2008. Database records as a surrogate for sampling effort provide higher species richness estimations. *Biodiversity and Conservation,* 17**,** 873-881.

MATTHEWS, J. W. 2004. Effects of site and species characteristics on nested patterns of species composition in sedge meadows. *Plant Ecology,* 174**,** 271-278.

MATTHEWS, T. J., COTTEE-JONES, H. E. W. & WHITTAKER, R. J. 2015. Quantifying and interpreting nestedness in habitat islands: a synthetic analysis of multiple datasets. *Diversity and Distributions,* 21**,** 392-404.

MCGEOCH, M. A. & GASTON, K. J. 2002. Occupancy frequency distributions: Patterns, artefacts and mechanisms. *Biological Reviews of the Cambridge Philosophical Society,* 77**,** 311-331.

MURRAY-HUDSON, M., LANE, C. R., NORTH, S. & BROWN, M. T. 2012. Macrophyte Species Distribution, Indices of Biotic Integrity, and Sampling Intensity in Isolated Florida Marshes. *Wetlands,* 32**,** 449-460.

NEKOLA, J. C. & WHITE, P. S. 1999. The distance decay of similarity in biogeography and ecology. *Journal of Biogeography,* 26**,** 867-878.

NICOLET, P., BIGGS, J., FOX, G., HODSON, M. J., REYNOLDS, C., WHITFIELD, M. & WILLIAMS, P. 2004. The wetland plant and macroinvertebrate assemblages of temporary ponds in England and Wales. *Biological Conservation,* 120**,** 261-278.

NILSSON, C., BROWN, R. L., JANSSON, R. & MERRITT, D. M. 2010. The role of hydrochory in structuring riparian and wetland vegetation. *Biological Reviews,* 85**,** 837-858.

OERTLI, B., AUDERSET JOYE, D., CASTELLA, E., JUGE, R., CAMBIN, D. & LACHAVANNE, J. B. 2002. Does size matter? The relationship between pond area and biodiversity. *Biological Conservation,* 104**,** 59-70.

PEINTINGER, M., BERGAMINI, A. & SCHMID, B. 2003. Species-area relationships and nestedness of four taxonomic groups in fragmented wetlands. *Basic and Applied Ecology,* 4**,** 385-394.

POLLOCK, M. M., NAIMAN, R. J. & HANLEY, T. A. 1998. Plant species richness in riparian wetlands - A test of biodiversity theory. *Ecology,* 79**,** 94-105.

R CORE TEAM 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

REED, P. B. J. 1988. *National list of plant species that occur in wetlands: national summary,* Biol. Rep. 88(24), U.S. Fish Wildlife Service.

REY BENAYAS, J. M., COLOMER, M. G. S. & LEVASSOR, C. 1999. Effects of area, environmental status and environmental variation on species richness per unit area in Mediterranean wetlands. *Journal of Vegetation Science,* 10**,** 275-280.

RODRIGUES, A. S. L. & GASTON, K. J. 2001. How large do reserve networks need to be? *Ecology Letters,* 4**,** 602-609.

ROLON, A. S., LACERDA, T., MALTCHIK, L. & GUADAGNIN, D. L. 2008. Influence of area, habitat and water chemistry on richness and composition of macrophyte assemblages in southern Brazilian wetlands. *Journal of Vegetation Science,* 19**,** 221-228.

ROLON, A. S. & MALTCHIK, L. 2006. Environmental factors as predictors of aquatic macrophyte richness and composition in wetlands of southern Brazil. *Hydrobiologia,* 556**,** 221-231.

ROLON, A. S., ROCHA, O. & MALTCHIK, L. 2012. Do effects of landscape factors on coastal pond macrophyte communities depend on species traits? *Aquatic Botany,* 103**,** 115-121.

ROSENZWEIG, M. L. 1995. *Species Diversity in Space and Time,* 40 West 20th Street, New York, NY, Cambridge University Press.

SHI, J., MA, K., WANG, J., ZHAO, J. & HE, K. 2010. Vascular plant species richness on wetland remnants is determined by both area and habitat heterogeneity. *Biodiversity and Conservation,* 19**,** 1279-1295.

SMITH, L. M. & HAUKOS, D. A. 2002. Floral diversity in relation to playa wetland area and watershed disturbance. *Conservation Biology,* 16**,** 964-974.

SOBERON, J. & PETERSON, A. T. 2004. Biodiversity informatics: managing and applying primary biodiversity data. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences,* 359**,** 689-698.

SOININEN, J., MCDONALD, R. & HILLEBRAND, H. 2007. The distance decay of similarity in ecological communities. *Ecography,* 30**,** 3-12.

THOMAZ, S. M., SOUZA, D. C. & BINI, L. M. 2003. Species richness and beta diversity of aquatic macrophytes in a large subtropical reservoir (Itaipu Reservoir, Brazil): the influence of limnology and morphometry. *Hydrobiologia,* 505**,** 119-128.

TJØRVE, E. 2003. Shapes and functions of species-area curves: a review of possible models. *Journal of Biogeography,* 30**,** 827-835.

TRIANTIS, K. A., GUILHAUMON, F. & WHITTAKER, R. J. 2012. The island species-area relationship: biology and statistics. *Journal of Biogeography,* 39**,** 215-231.

ULRICH, W. & GOTELLI, N. J. 2012. A null model algorithm for presence-absence matrices based on proportional resampling. *Ecological Modelling,* 244**,** 20-27.

WHITTAKER, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs,* 30**,** 280-338.

WILSON, D. & PATON, D. C. 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.

Statement of authorship Chapter 3

Chapter 3   Niche constraints and competition moderated by short-distance dispersal structure wetland plant communities

Abstract

Sites that contain relatively unique species compositions within a region are important to identify as the risk of regional species loss from such sites can be high. Variation in β-diversity—differences in species composition among sites—can be used to identify regionally unique species combinations and the environmental conditions that create them. Wetland plant communities provide good opportunities for studying community assembly, because β-diversity often accounts for more than half of regional species diversity. Previous studies of wetland plant community assembly have found contrasting results for the primary drivers of species composition. I tested the support for three main assembly mechanisms in seasonal wetland plant communities using an information-theoretic framework. I hypothesised that if species composition depends on: (*i*) niche availability, then wetlands with more diverse environmental conditions (e.g., hydrology, soil type) should have more unique compositions due to increased niche dimensions; (*ii*) competition, then dominance by relatively few, competitively superior species should make species composition more similar among wetlands; (*iii*) dispersal, then wetlands with the highest propagule availability (measured as proximity to external sources) should have the most diverse compositions. Model-averaged regression coefficients indicated comparable effect sizes for all three processes, indicating that all three processes operate in determining the species composition of South Australian wetland complexes. Increased competition constrained species composition to the best competitors as I predicted. Niche-effects constrained the potential species pool, producing similar communities in wetlands dominated by permanent saturation or highly acidic soils. High local dispersal potential

increased similarity—opposite to my prediction—possibly by increasing the immigration probability of superior competitors, which then limits further immigration by other species. More unique wetland communities occurred where conditions suited a larger fraction of the regional species pool, but only if competition was not limiting, which appears to depend on the probability of short-range dispersal. Since multiple assembly processes are involved, future wetland studies should no longer focus on testing support for a single mechanism for community assembly, but rather multiple and potentially interacting processes.

Introduction

Understanding the assembly processes that control the species diversity patterns of ecological communities can help identify the best conservation strategies to maintain them under global change. As the link between local and regional diversity (Whittaker, 1960, Tuomisto, 2010) β-diversity, which is measured as the change in species composition between sites, provides a means to connect biological patterns to underlying processes. For example, regional β-diversity can be partitioned into a site-level indicator of comparative uniqueness in species composition (Legendre and De Caceres, 2013), which can be analysed as a metric of the relative role of competing assembly mechanisms. Wetlands are a good model system to investigate community assembly using this approach, particularly because β-diversity tends to be high (Peintinger et al., 2003, Freestone and Inouye, 2006, Sasaki et al., 2012), on average accounting for almost 80% of partitioned gamma (regional-scale) species diversity (data in Table 1.1, Chapter 1). Community assembly processes can be divided into three main classes emphasising the roles of the niche, biological interactions (e.g., competition) and dispersal (Hubbell, 2001, Vellend, 2010, Chase and Myers, 2011, Hille Ris Lambers et al., 2012).

Niche-based explanations of species assembly (e.g., Hutchinson, 1957, Macarthur

and Levins, 1967, Leibold, 1995) and β-diversity (e.g. Tuomisto et al., 2003, Cottenie, 2005) emphasise the role of environmental heterogeneity and species-level differences in relative fitness. Species form into limited membership communities constrained by the availability of their ideal conditions and the outcome of competition for limited resources (Tilman, 1997, Hubbell, 2001, Leibold et al., 2004). A highly influential niche constraint in wetlands is, of course, the availability of water. Vascular plants select different areas within continuum of hydrological conditions (Silvertown et al., 1999) and this is particularly evident in wetland species where plant composition and zonation is constrained to sites offering suitable hydrological properties (Grace and Wetzel, 1981, Brock and Casanova, 1997, Casanova and Brock, 2000, Thomaz et al., 2003, Douda et al., 2012). Wetlands that provide the most diverse range of hydrological conditions often have the highest species richness (e.g., Brose, 2001, Shi et al., 2010, Shi et al., 2013). A wide range in hydrology— from short-term surface saturation to permanent inundation along with a range of intermediate depth and duration combinations—should promote increased wetland species diversity. This can potentially lead to more unique species compositions when compared to wetlands with a smaller hydrological range because a larger fraction of the regional species pool will find suitable habitat.

Coexistence within a community depends not only on species' niche differences, but also on differences in relative fitness (Chesson, 2000, Hille Ris Lambers et al., 2012). If several species with a strong overlap in ideal niche conditions are present, competitive exclusion is predicted to remove inferior species that are too functionally similar (Hille Ris Lambers et al., 2012). Hence wetland plant zonation and composition also reflect the outcome of competition for space among plants with similar hydrological requirements (Grace and Wetzel, 1981, Lenssen et al., 1999). Many wetland plant species spread vegetatively (Santamaria, 2002) and form monospecific stands that reduce wetland species

diversity (Lavergne and Molofsky, 2004, Zedler and Kercher, 2004). Competitive exclusion in wetlands dominated by a few such species would act to offset any increase in species diversity resulting from broader hydrological niche dimensions. Wetland communities dominated by superior competitors should therefore be relatively similar in composition and contribute little to regional species richness.

In contrast to niche-based processes, dispersal-based explanations of β-diversity patterns (e.g., Hurtt and Pacala, 1995, Condit et al., 2002) do not distinguish between sites in terms of suitability, or between species according to relative fitness differences. In exclusively dispersal-driven assembly, species composition represents a balance between colonisation and extinction (Hubbell, 2001). Propagule dispersal is important for both compositional similarity and species richness in wetlands (Chapter 2; Flinn et al., 2010, Calcada et al., 2013), particularly via hydrochory (Nilsson et al., 2010). As predicted under island biogeography (MacArthur and Wilson, 1967), isolated wetlands tend to have fewer species than expected for their size (e.g., Boughton et al., 2010, O'Connell et al., 2013), suggesting that dispersal constraints limit species' distributions from reaching sites where potentially suitable habitat is available. In a dispersal limited environment, only strong dispersers should be able to reach more remote wetlands, which should increase their similarity because of the smaller pool of species that have this trait. Conversely, wetlands that are better connected to other source populations should have the highest seed arrival and therefore species richness (Myers and Harms, 2009, Boughton et al., 2010). As β-diversity is partly a result of differences in species richness (Koleff et al., 2003), highly connected, more diverse wetlands should also contribute more to regional diversity than more isolated, lower richness wetlands.

Dispersal assembly assigns more importance to stochastic mechanisms such as ecological drift and chance colonisation or extinction in structuring communities (e.g.

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Hubbell, 2001, Chase, 2010), whereas niche-based assembly assumes species compete for and ultimately occupy their most suitable areas. The results of recent studies relating to community assembly processes in wetlands have been equivocal, finding biological interactions (Chmara et al., 2013), dispersal (Boughton et al., 2010) or niche-related processes (Flinn et al., 2010, Douda et al., 2012) are dominant. Some have also suggested contributions from more than one process, but have tended to focus on trying to detect evidence for one of these at a time . In contrast, I consider all three assembly processes simultaneously, comparing support for each in a wetland system.

I used plant survey data from a network of seasonal wetlands in temperate South Australia. I tested support for hypotheses of niche availability, competitive exclusion and dispersal. I hypothesised that: (*i*) if niche-based assembly exerts the dominant influence on species composition, sites with the widest range of environmental conditions (e.g., heterogeneity in hydrological or soil conditions) should have the most unique species compositions; (*ii*) if niche-based assembly results in more species with overlapping niche requirements, then composition will depend on competitive processes; and (*iii*) if community assembly is dispersal-limited, then wetlands that are are more connected to other wetlands should have the most unique composition because they will have the most diverse and abundant propagule supply. Furthermore, I expected that seasonal water limitations due to the prevailing Mediterranean climate would result in hydrology having the strongest influence on composition—specifically that relatively permanent wetlands would support species that cannot persist in the more typical, seasonal wetlands, resulting in more unique species composition in the former. I found some support for niche-related influence on species composition, where harsher conditions limited the number of species from the regional species pool able to colonise the site. Moreover, short-distance dispersal and competitive exclusion appear to be at least as influential on community assembly and

possibly interact via a sampling effect for competitively superior species.

Methods

Data sources

I analysed a field survey dataset describing wetlands of the Fleurieu Peninsula, South Australia (Fig. 3.1). Data were collected in autumn 2006 to classify major vegetation associations (Stevens, 2006). I selected 26 wetlands with a consistent sampling effort, each surveyed using five quadrats. Quadrats (5 × 2 m) were located along transects oriented in the direction of the major hydrological gradient to sample the range in hydrological niche space. Quadrat-long axes were oriented along contours of the hydrological gradient (perpendicular to transects) and spaced systematically at regular intervals 20-50 m apart. Actual spacing was selected subjectively to sample variation in broad structure and composition, while avoiding wetland edges.

The sampling design (five samples spaced along along a water availability gradient) provides inference on species composition and density (number of species per 50 m^2; Gotelli and Colwell, 2001) across the hydrological gradient at each wetland. However, as quadrat spacing varied among wetlands (mean [±95 % confidence limits] of the distance between the most distant quadrats = 207 [145, 269]), communities that were sampled with more widely spaced quadrats could have more diverse communities simply due to reduced spatial autocorrelation. I thus tested did *a priori* checks for any relationship between sampling extent and species diversity, finding no evidence that differences in sample spacing affect β-diversity (Pearson's $r = 0.14$, $t_{23} = 0.66$, $p = 0.52$) or total wetland species richness (Pearson's $r = 0.15$, $t_{23} = 0.74$, $p = 0.46$). I conclude from this analysis that no bias

was introduced and samples provide a comparable means to infer differences in community structure across the hydrological gradient present in each wetland.
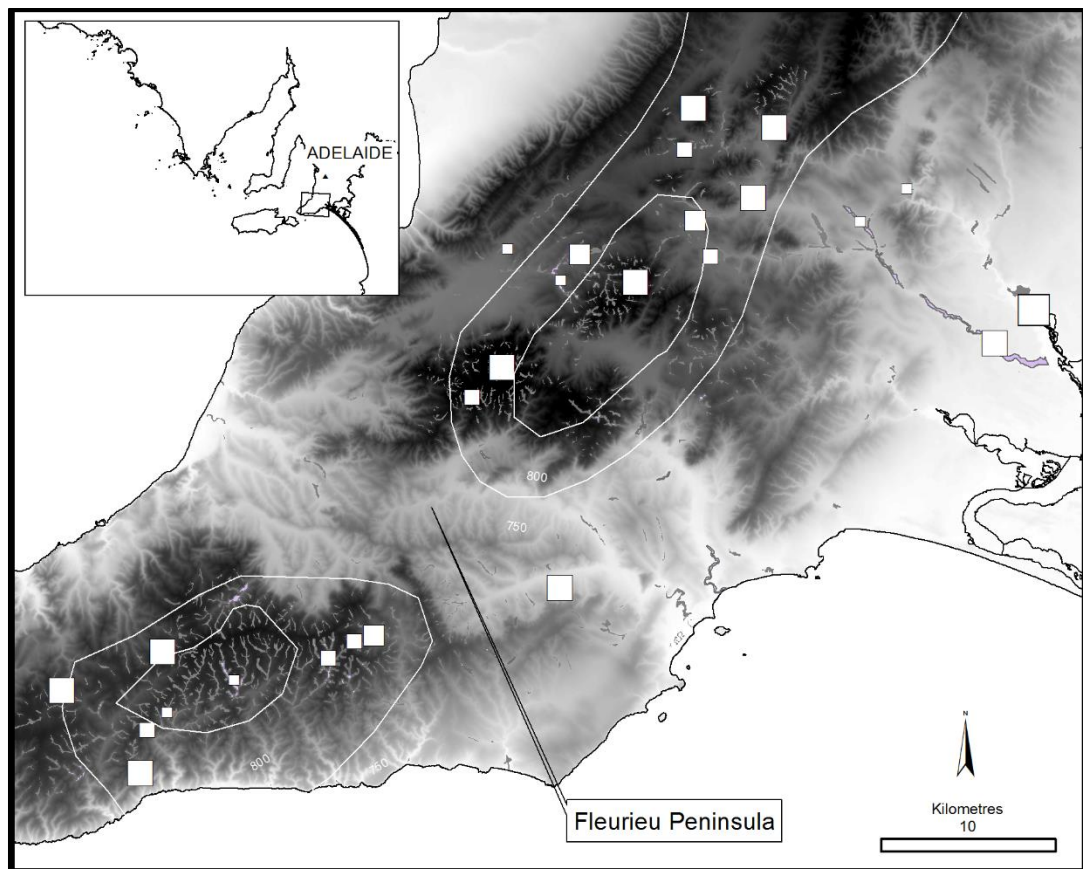
Figure 3.1 Fleurieu Peninsula, South Australia, with wetlands coded according to their local contribution to β-diversity, where larger symbols represent wetlands with more unique species compositions. Shading represents elevation, with dark areas indicating higher areas that reach a maximum of ~ 320 m above sea level. Also shown are the 750 and 800 mm rainfall isohyets

I calculated the mean and coefficient of variation for each variable over the five quadrats to create wetland-scale measures of environmental patterns and their variability. For the vegetation analysis, I converted cover scores to percentage cover representing mid-points of each cover class. I removed exotic species from all analyses, but retained terrestrial species (Chapter 2). Taxonomic resolution was to species level, and cover of each species was recorded in the field using a modified Braun-Blanquet scoring system (Braun-Blanquet, 1932). Biomass was measured independently of the taxonomic data using a touch pole method. The number of touches within a conceptual 5 cm-diameter vertical cylinder discretised to 0.2 m segments was recorded at 20 points spaced 0.25 m apart along the central axis of the quadrat. In addition to spatial coordinates of quadrat centroids, vegetation cover and biomass, field data included several environmental measurements: soil moisture according to a seven-level ordinal scale representing conditions from dry to completely inundated; presence/absence of peat soil substrates (indicative of permanent, long-term saturation), and, soil pH recorded to the nearest 0.5 pH unit using a colorimetric method.

Response and predictor variables

To test the different mechanisms leading to compositional changes between sites, I calculated or derived over 40 environmental variables (Table 3.1) using spatial data on wetland shape, soil type, topography, hydrology, roads, land use and native vegetation cover in polygon or raster format, analysing these using a 400 m buffer around each wetland. Owing to the proximity of wetlands in the region (mean distance to the ten nearest wetlands = 1494 m; median = 963 m; Fig. 3.1), larger buffers (e.g., 1 km) did not discriminate well between wetlands. I used the 'Intersect' or 'Zonal Statistics' tools in ESRI ArcGIS (Version 10.2) software for polygon and raster analysis, respectively. My strategy for selecting variables was to provide good representation across the mechanisms

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of niche-based (e.g., hydrology and other physiographic variables affecting either conditions or resource availability), dispersal-based (i.e., the density, area and proximity of wetlands and native vegetation), and biological interactions (e.g., cover of exotic species, biomass). I also included the length of roads (m/ha) and land use as indicators of disturbance. I centred and re-scaled all input variables by two standard deviations (i. e., $x' = (x - \overline{x})/2.\sigma_x^2$) to allow direct comparison of effect sizes in model-averaged coefficients among binary (unscaled) and continuous predictors (Gelman, 2008).

Table 3.1 Full list of all environmental variables calculated for analysis. Those shown in bold were included in the final modelling dataset, with others removed due to collinearity (with a threshold being any value for Pearson's $|r| > 0.6$).

Mechanism	Abbrev	Description, units and rationale
Niche	**soil pH**	**Mean soil hydrogen ion concentration from all wetland quadrats (range in unstandardised pH units 5.1–8.5).**
Niche	**peat**	**Percentage of wetland samples with peat substrate. Peat soils can only form under permanent saturation, hence this is a reliable indicator of those conditions (range 0-100)**
Niche	**soil.G**	**Percentage of wetland buffer zone area containing soils classified as soil group G (see Table 3.2 for a description of each soil group)**
Dispersal	**% wetland**	**Percentage of wetland buffer zone area occupied by wetlands other than the site under analysis (range 0-30)**
Dispersal	**wetland count**	**The higher the number of wetlands within a short distance the higher the probability the target wetland can receive a wide range of propagules. Integer count of wetlands within a 200 m buffer of the wetland outline (range 1 - 7). Treated as a continuous variable in analysis.**
Dispersal	**ave5**	**Mean centroid-centroid distance to the nearest five wetlands**
Biological	**ExCov**	**Mean % cover of exotic species present in the quadrat (range 0-23)**

Mechanism	Abbrev	Description, units and rationale
interaction		
Biological interaction	**biomass**	**Average of the total number of touch pole hits for the quadrats in each wetland (range 20-136)**
Niche	**rf**	**Mean annual rainfall in mm – integer variable**
Niche	**hydAve**	**Quadrats were given integer wetness scores based on a squeeze test of substrate (range 1 – 7). hydAve is the arithmetic mean of these values for the wetland and provides a measure of relative levels of wetness.**
Niche	**hydHet**	**Coefficient of variation in hydrological index scores. A measure of within-wetland hydrological heterogeneity**
Niche or dispersal	order	Strahler stream order, a surrogate for catchment size. Low numbers indicate head water streams. Integer variable
Dispersal	CM.XXX	where XXX = Too, Fin, Myp or Bal indicating different catchments with multiple (> 3 wetlands) in the dataset and expected to have higher similarity (Chapter 2) due to common streamflow regimes and hydrochory
Biological interaction	cons	binary variable indicating wetland catchment is under a formal conservation agreement or is located within a conservation reserve

Mechanism	Abbrev	Description, units and rationale
Biological interaction	**graze**	**Binary variable indicating that grazing was present in the surrounding catchment. By selectively removing preferred fodder plants, this alters competitive processes**
Biological interaction	forest	High proportion (>50%) of plantation forest in catchment (not used as only one wetland was under this landuse)
Dispersal	**pcNV**	**Percentage of wetland buffer area comprising any form of non-wetland remnant native vegetation. Provides an indication of the likely density of native terrestrial propagules.**
Dispersal/ biological	**lenRd**	**Linear road length within wetland buffer area. Roads have been found to degrade wetland condition including through effects on richness and number of exotic species. Continuous variable in units of km/km-2**
Random sampling	area	Continuous variable in hectares
Random sampling	per	Simple measure of wetland dimensions alternative to area. Of interest for the same reasons as irregularity.

Mechanism	Abbrev	Description, units and rationale
Random sampling	dCir	Ratio of a circle with area the same as the wetland and observed wetland perimeter length. A relative measure of how irregular the wetland planform is.
Niche	**soilHet**	**Integer variable recording the number of soil types mapped to the wetland and buffer area. Range 3-7, treated as continuous variable.**
Niche	**soil.X**	**where X = F, G, I, K or N indicating soil group, scored as the % of wetland and buffer area. General characteristics are F soil.N is associated with fertility; soil.I. Only G and I were not collinear and used in analysis**
Niche	**elev**	**Mean wetland height above sea level in metres.**
Niche	elvRng	Maximum – minimum elevation – an indication of the range in conditions and likely topographic variability within the wetland.
Niche	slope	Mean slope of the wetland and surrounding 200 m buffer. Indicative of variation in landform (%)
Niche	**slope.cv**	**Microtopographic variability interacts with hydrology to increase habitat complexity and hydrological niche width.**

Mechanism	Abbrev	Description, units and rationale
Biological interaction	wCov	Data include cover from multiple strata and can sum to more than 100 %. This value provides a measure of the total biomass present in each sample in a wetland and a surrogate indicator of biological competition.
Biological interaction	**cvBM**	**Coefficient of variation in wBM – indicating how variable the vertical strata were across all quadrats**

I tested all variables for collinearity removing those with the least plausible biological relationship with one of the three hypotheses. β-diversity between two sites results from differences in composition, so it must be taken into account when there are differences in total species richness between them (Koleff et al., 2003). To ensure any influence of the environmental predictors was due to their effects on species composition, and not total species richness, I therefore also tested for any linear correlation between each predictor and wetland species richness.

Table 3.2 Soil group broad characteristics (Hall et al 2009)

Grp	Name	pH	Fertility	Water holding capacity	Drainage	Comments
F	Deep loamy texture-contrast	neutral-acidic	mod - high	mod	mod	very common in region; associated with perched watertables
G	Sand over clay	strongly acidic in high rainfall areas	low - mod	mod	mod	more common in east of region; associated with perched watertables
I	Highly leached sands	acidic	low	mod	good	Uncommon in region; valley floors only
K	Acidic soils on rock	acidic	mod	mod	low – mod	Form in weathering basement rock; common in uplands in region; perched watertables
N	Wet soils	acidic in high rainfall areas	mod - high	high	low	Common wetland soils; includes peat

I used pairwise Bray Curtis (Bray and Curtis, 1957) dissimilarity as a measure of total β-diversity. As a response variable, I quantified the regional uniqueness in species

composition for each wetland using the 'local contribution to β-diversity' metric (Legendre, 2014), which partitions total β-diversity into a vector of site-level contributions. Technically, the local contribution to β-diversity is the ratio of the squared distance of each sampling unit to the centroid of the distribution (the site-level sum of squares) and the total sum of squares for the community dissimilarity matrix (Legendre and De Caceres, 2013).

Model structure

I built three subsets of models, each using only variables that were proxy measures for one of the three hypotheses. That is, I did not combine niche-based predictors with those measuring dispersal or competition in a single model. I built models using linear, quadratic and interaction terms where unimodal (hump-shaped) or multiplicative relationships were biologically plausible for the variables concerned. To avoid overfitting, I used three or fewer predictors in any one model to maintain a ratio of data to predictors close to 10. I combined all models into a single candidate set of 50 models for comparison and ranking.

In addition to the three main mechanistic hypotheses under test, I also considered two possible confounding mechanisms: passive sampling where larger wetlands attract more rare species and therefore have more unique composition simply because they represent a larger target (Connor and McCoy, 1979) and spatial autocorrelation where nearby sites are more similar because of their proximity (Brown, 1984). I fit models for area, wetland size and shape including these in the candidate set to test for passive sampling effects. To test for spatial dependency in vegetation composition, I used a Mantel test of Euclidean distances in XY grid coordinates (UTM Easting and Northing) and the local contributions to β-diversity.

I also tested for non-linear spatial relationships using principal coordinates of neighbour matrices (PCNM; Borcard and Legendre, 2002), calculated with R package 'vegan' (Oksanen et al., 2013). As there was no *a priori* biological rationale to build

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candidate models based on spatial dependencies, I instead used a two-step process. I used

all 16 principal coordinates of neighbour matrices eigen functions to build a candidate set

of univariate spatial models against the local contributions to β-diversity vector. I selected

all variables in the 95% confidence set, yielding four principal coordinates of neighbour

matrices. However, I found strong linear correlations with at least one environmental

predictor for all of these variables (Pearson's $|r| > 0.6$) and as a result I did not include any

pure spatial variables in the candidate set. I provide a list of the environmental variables,

the model structures and their biological rationale in Table 3.3.

Table 3.3 Candidate model set explained in terms of predictors and biological rationale

Mechanism	name	par1	par2	par3	Rationale for effect on wetland plant composition
Niche – based (Hydrological)	hyd00	slope.cv	-	-	coefficient of variation of slope provides a measure of microtopographic variations that can increase hydrological niche dimensions
	hyd01	hydAve	-	-	hydrology is the dominant environmental condition in structuring wetland communities
	hyd02	hydAve	hydHet	-	hydrology will have different effects on mean uniqueness dependent upon pH
	hyd03	hydAve	slope.cv	hydAve:slope.cv	combined effects of mean water availability and number of microtopographic niches
	hyd04	hydHet	-	-	hydrological heterogeneity has an independent affect on composition
	hyd05	hydHet	slope.cv	-	combined effects of measured hydrological and microtopographic variability
	hyd06	hydHet	peat	hydHet:peat	interactive effects of high water permanence (indicated by peat) and hydrological heterogeneity

Mechanism	name	par1	par2	par3	Rationale for effect on wetland plant composition
	hyd07	rf	hydAve	-	tests the importance of different water sources: high rainfall increases likelihood of perched wetlands, while mean water availability measures groundwater supply
	hyd08	hydHet	rf	hydHet:rf	As for hyd07, but allowing for multiplicative effects of heterogeneity and perched water supplies
	hyd09	slope.cv	rf		As for hyd07 hyd08, but allowing for effects of topographic heterogeneity and rainfall
	hyd10	rf	hydAve	hydHet	As for hyd07, but including local water supply heterogeneity
	hyd11	hydAve	hydAve^2		increasing wetness has a unimodal (hump shaped) relationship with compositional uniqueness
Niche-based (Physiographic)	phy01	soilHet	soil pH-	-	The more soil types present, the larger the range of conditions that are present but soil pH limits composition independently
	phy02	soil pH	soilTypeG	peat	Soil type G is of lowest fertility which has been associated with unique wetland plant communities. Peat and pH are strong hydrological and physiological niche determinants respectively.

Mechanism	name	par1	par2	par3	Rationale for effect on wetland plant composition
	phy03	slope.cv	soilTypeG	peat	The coefficient of varation in slope is a measure of local topographic irregularity creating different micro-habitats, that can also vary depending on elevation
	phy04	slope.cv	soil pH	-	soil pH is a niche axis; micro-topographical varaitions can help to moderate this providing wetter micro-sites.
	phy05	slope.cv	-	-	microtopographic variation is the major determinant of habitat heterogeneity
	phy06	soil pH			soil pH is known to influence species performance and preferred niche conditions
	phy07	slope.cv	soil pH	slope.cv:soil pH	Both soil pH and microtopographic variation should increase habitat heterogeneity
	phy08	elevation	soilHet	elevation:soilHet	As for phy05, explicitly including soil type variability
	phy09	soilTypeG	elevation	soilTypeG:elevation	As for phy02 and phy05, allowing a multiplicative effect

Mechanism	name	par1	par2	par3	Rationale for effect on wetland plant composition
	phy10	soil pH	elevation	soil pH:elevation	As for phy09
	phy11	elevation	slope.cv	slope.cv:elevation -	elevation is correlated with rainfall and soil properties, topographic variation and land clearance history and may explain much of the variation in species composition
Biological interactions	bio01	biomass	-	-	Tests for a simple linear relationship between competition (biomass) and uniqueness
	bio02	biomass	biomass^2	-	As for bio01, but allowing a unimodal response function. That is, where biomass only becomes limiting above some competitive threshold
	bio03	biomass	exCover	-	Testing separate linear effects of exotic plant cover and total biomass
	bio04	exCover	-	-	Tests for a simple linear effect of exotic plant competition
	bio05	graze	-	-	Testing separate effects of exotic plant cover and biomass removal from grazing
	bio06	conservation	-	-	Testing separate effects of exotic plant cover under a conservation land use where biomass removal is likely to be low
	bio07	biomass	conservation	length of road	Testing for linear or multiplicative effects of landuse and competition
	bio08	biomass	graze	length of road	Testing for linear or multiplicative effects of landuse and competition
	bio09	biomass	graze	biomass:graze	Testing for linear or multiplicative effects of road

Mechanism	name	par1	par2	par3	Rationale for effect on wetland plant composition
					disturbance and conservation land management. (Road length in wetland buffers has been associated with reduced species richness)
	bio10	biomass	conservation	biomass:conservation	Testing for linear or multiplicative effects of road disturbance and biomass disturbance
	bio11	lengthRd	biomass	lenRd:biomass	Testing for linear or multiplicative effects of road disturbance on biomass
	bio12	lengthRd			Testing for a single linear effect of road length on composition (likely to be through effects on richness)
Dispersal-based	dsp01	pcNV	-	-	Testing for a linear area-based effect of terrestrial native plant propagule density from nearby remnant patches of native vegetation
	dsp02	pcWet	-	-	As for dsp01, but testing for wetland plant propagules
	dsp03	wetCount	-	-	Testing whether increased numbers of discrete wetland patches in buffer zones increases community uniqueness from a passive sampling effect
	dsp04	wetCount	ave5	-	As for dsp03, but also testing whether wetland area and number have an effect on composition

Mechanism	name	par1	par2	par3	Rationale for effect on wetland plant composition
	dsp05	wetCount	pcNV	wetCount:pcNV	As for dsp01 and dsp03, but allowing a multiplicative effect of area and number of wetlands
	dsp06	wetCount	ave5	wetCount:ave5	Testing for an effect of isolation (ave5) and nearby dispersal (wetCount) success – as for dsp04, but allowing interaction effect
	dsp07	pcNV	ave5	pcNV*ave5	Testing for the influence of nearby native (non-wetland) vegetation and longer distance proximity
	dsp08	ave5	-	-	Testing for intermediate level isolation effects. Mean centroid-centroid distance of the nearest five wetlands
	dsp09	catch	pcWet	pcNV	Testing for within catchment uniqueness, possibly due to a combination of history, source populations and flow hydrology; plus effect of propagule sources
	dsp10	catch	-	-	Testing for within catchment uniqueness, possibly due to a combination of history, source populations and flow hydrology.
	dsp11	ave5	$ave5^2$	-	Allowing for a unimodal effect of wetland isolation. That is wetland compositional uniqueness peaks at intermediate isolation distances.
Biogeographical	geo01	area	-	-	Tests of area on composition for equal sized sampling areas tests a prediction of species-area relationships and the presence of sink species only

Mechanism	name	par1	par2	par3	Rationale for effect on wetland plant composition in larger wetlands
	geo02	perimeter	-	-	Test of passive sampling-a larger perimeter provides a larger target for propagules
	geo03	dCir	-	-	As for geo02, but testing the effect of an irregular outline rather than a larger target zone. Hence also includes the possibility of increased microhabitat availability in irregular wetland planform

Model fitting

Local contributions to β-diversity take values from 0 to 1, so I used beta regression (Ferrari and Cribari-Neto, 2004) to fit the candidate set of models. Beta regression, based on the two-parameter beta distribution, was proposed by Ferrari and Cribari-Neto (2004) to model variables that are constrained to the unit interval (0, 1) such as proportional data. It is similar in form to generalised linear models, with the response variable modelled via a link function (usually the logit) and a linear predictor, with the model optimised via maximum likelihood (Ferrari and Cribari-Neto, 2004). Simas et al. (2010) extended the model to incorporate a precision parameter ϕ that allows for dispersion to be modelled as a function of covariates via a separate link function and linear predictor. I did not attempt the latter because I had no biological basis to do so, and instead allowed the ϕ parameter to be a fitting constant. I did all beta regression using R package 'betareg' (Cribari-Neto and Zeileis, 2010).

Model comparison and inference

I compared and ranked models using Akaike's information criterion corrected for small sample size (AIC$_c$; Burnham and Anderson, 2002, Grueber et al., 2011). I selected all models within 4 AIC$_c$ of the top-ranked model as a final model set for model averaging (Burnham and Anderson, 2002, Grueber et al., 2011). I calculated model-averaged coefficient values across all models in the final set based on wAIC$_c$ using the zero method, recommended when the aim is to determine which predictors have the strongest effect on the response variable (Grueber et al., 2011, Nakagawa and Freckleton, 2011). In the zero method, each coefficient is averaged as though the predictor were present in every model and the coefficient value is set to zero if it does not appear. I inferred support for the different hypotheses based on both the identities of predictors in the final model set and

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their averaged coefficient values. I calculated standard errors and 95% confidence intervals (using a normal approximation) for parameter estimates based on the unconditional variance, which accounts for model uncertainty (Burnham and Anderson, 2002).

I did all modelling and analysis in the R language (R Core Team, 2014) using packages 'arm', 'betareg', 'vegan' and 'MuMIn' as described above (Cribari-Neto and Zeileis, 2010, Oksanen et al., 2013, Barton, 2014, Gelman and Su, 2015) and plotting package 'ggplot2' (Wickham, 2009). I also used the custom R function 'LCBD.comp' provided in Legendre (2014) to calculate the local contributions to β-diversity.

Results

Total observed species richness was 113 native and 17 exotic vascular plant species. Mean native species richness for quadrats and wetlands was (mean [± 95% confidence limits]) 8.7 [8.03, 9.34] and 21 [17.8, 23.3], respectively. Wetland species density had a weak negative correlation with total area of the wetland being sampled (Pearson's r = -0.36, t_{23} = -1.8481, p = 0.08), but local contributions to β-diversity (range: 0.029-0.055) were not correlated with native species richness (Pearson's r = -0.23, t_{23} = -1.14, p = 0.26), nor the spatial proximity of wetland centroids (Mantel test r = 0.06, p = 0.13). Mapping of local contributions to β-diversity suggests more compositionally unique wetlands (those with higher local contribution to β-diversity scores) tended to be located away from areas where dense clusters of wetlands occur, but relatively unique sites were distributed throughout the region (Fig. 3.1).

The difference in AIC_c from the top- to bottom-ranked candidate models was 13.6. A subset of models containing > 95% of total model Akaike weights (the 95 % confidence set) included 23 models (Table 3.4). I instead selected all models within 4 AIC_c of the top-ranked model, each also having Akaike weights of at least 0.05. This yielded a final set of 7

models used in model-averaging, three based on dispersal (including the top-ranked model; $w\text{AIC}_c = 0.25$; 2.3 times more support than the next ranked) and two each supporting niche and competitive hypotheses (Tables 3.4-3.6). Deviance explained by models in the final model set ranged from 0.20–0.40 (Table 3.5).

I averaged across the final model set which included 8 predictors, none of which was correlated with species richness (Pearsons's r range: -0.27—0.12; p range: 0.17-0.98; d.f. = 24; Table 3.7). The top-ranked model included only a single predictor of dispersal (*Wetland count* – the number of other wetlands within 400 m; Table 3.1-3.3). This predictor also had the strongest effect size according to the model-averaged regression coefficients ($\hat{\beta}_{wc} \pm \text{S.E.} = -0.106 \pm 0.12$; Table 3.6). The predictors *total biomass* (representing competition) and *peat substrates* (indicating permanent saturation or inundation) also had negative effects on composition, although with smaller effect sizes ($\hat{\beta}_{bm} = -0.055 \pm 0.094$; $\hat{\beta}_{pt} = -0.016 \pm 0.049$). Predictors that were associated with increasing uniqueness in composition (i.e., had positive coefficients on local contribution to β-diversity) were *soil pH*, *exotic plant cover* and the *proportion of soil type G* (Table 3.6) found in the wetland buffer area ($\hat{\beta}_{ph} = 0.029 \pm 0.070$; $\hat{\beta}_{ex} = 0.018 \pm 0.051$; $\hat{\beta}_{sg} = 0.014 \pm 0.045$). Predictor importance values suggested a similar order of relative influence for predictors with *wetland count* (0.24), *biomass* (0.15) and *exotic cover* (0.15) the three highest-ranked (Table 3.6).

Table 3.4 Model selection table for full candidate set ranked by Akaike's information criterion corrected for small sample size (AICc), with the weight and difference between each model and the top-ranked model. The evidence ratio is the ratio of the Akaike weight for the top-ranked model and the model being compared. Model name codes indicate which hypothesis the predictors used to build the model are testing: niche mechanisms are represented by prefix *hyd* for hydrological or *phy* for physiographic predictors; *dsp* = dispersal; *bio* = biological interactions. *k* is the number of parameters in each model.

Model	k	AIC_c	$wAIC_c$	ΔAIC_c	Evidence ratio
dsp03	3	-183.9	0.25	0	1
bio03	4	-182.3	0.11	1.67	2.31
bio01	3	-182.2	0.1	1.77	2.43
dsp04	4	-181.9	0.09	2.05	2.79
phy02	5	-181.6	0.08	2.29	3.14
phy06	3	-180.6	0.05	3.36	5.36
dsp02	3	-180.5	0.05	3.4	5.48
bio02	5	-179.7	0.03	4.27	8.48
bio04	3	-179	0.02	4.92	11.71
dsp06	5	-178.8	0.02	5.13	13.01
phy07	5	-178.7	0.02	5.2	13.48
dsp05	5	-178.6	0.02	5.31	14.22
phy11	4	-178.5	0.02	5.4	14.89
bio11	5	-178.4	0.02	5.49	15.56
phy04	4	-177.9	0.01	6	20.05
phy03	5	-177.9	0.01	6.07	20.79
phy01	4	-177.8	0.01	6.1	21.1
null	2	-177.1	0.01	6.82	30.19
bio09	5	-176.8	0.01	7.16	35.81
bio10	5	-176.7	0.01	7.24	37.35
dsp08	3	-176.6	0.01	7.37	39.79
bio07	5	-176.3	0.01	7.67	46.33
bio08	5	-176.3	0.01	7.68	46.48
phy05	3	-175.3	3.39E-03	8.63	74.99
hyd06	5	-175.2	3.20E-03	8.75	79.47
bio06	3	-175.2	3.17E-03	8.77	80.19

Model	k	AIC$_c$	wAIC$_c$	ΔAIC$_c$	Evidence ratio
hyd04	3	-174.9	2.76E-03	9.05	92.18
hyd01	3	-174.7	2.56E-03	9.2	99.42
dsp09	5	-174.6	2.45E-03	9.28	103.75
dsp01	3	-174.6	2.42E-03	9.31	104.96
dsp10	3	-174.6	2.42E-03	9.31	104.98
geo03	3	-174.6	2.41E-03	9.32	105.38
bio05	3	-174.6	2.38E-03	9.34	106.66
geo02	3	-174.6	2.35E-03	9.37	108.25
bio12	3	-174.6	2.34E-03	9.38	108.67
hyd00	3	-174.6	2.34E-03	9.38	108.76
geo01	3	-174.6	2.33E-03	9.38	109.01
dsp11	4	-174.1	1.89E-03	9.8	134.37
phy09	5	-173.8	1.58E-03	10.17	161.36
dsp07	5	-173.1	1.12E-03	10.85	226.9
hyd07	4	-172.9	1.02E-03	11.04	250.13
hyd09	4	-172.6	8.60E-04	11.38	295.46
hyd02	4	-172.4	7.83E-04	11.56	324.48
phy08	5	-172.3	7.49E-04	11.65	339.14
hyd05	4	-172.1	6.75E-04	11.86	376.34
hyd11	4	-171.9	6.29E-04	12	404.11
hyd03	5	-170.9	3.71E-04	13.06	685.18
hyd08	5	-170.4	2.99E-04	13.49	850.41
hyd10	5	-170.4	2.96E-04	13.51	857.3
phy10	5	-170.3	2.76E-04	13.65	919.96

Table 3.5 Final model set and model selection values. Model structure and rationale is given in Table 3.3; predictors are described in Table 3.1 and their standardised regression coefficients are given in Table 3.6. k is the number of predictors including the two intercepts from beta regression (subtract from 26 – the number of samples - to obtain model degrees of freedom); AIC_c is Akaike's second-order information criterion; $wAIC_c$ is the small sample corrected Akaike weight; ΔAIC_c is the difference in Akaike's second order information criterion compared with the minimum AIC_c; evidRat = evidence ratio, the ratio of the $wAIC_c$ of each model and the top ranked model. Pseudo-R^2 is the approximate amount of variation in the response variable explained by the model.

Code	k	AIC_c	$wAIC_c$	ΔAIC_c	evidRat	pseudo-R^2
dsp03	3	-183.9	0.25	0	1	0.31
bio03	4	-182.3	0.11	1.67	2.31	0.34
bio01	3	-182.2	0.1	1.77	2.43	0.26
dsp04	4	-181.9	0.09	2.05	2.79	0.33
phy02	5	-181.6	0.08	2.29	3.14	0.39
phy06	3	-180.6	0.05	3.36	5.36	0.20
dsp02	3	-180.5	0.05	3.4	5.48	0.21

Table 3.6 Regression coefficients for predictor variables in averaged model. Averaged regression coefficients (Estimate) were calculated using the zero method (Burnham and Anderson, 2002) and indicate relative effect size for the predictor. I.V. = average importance value (the sum of Akaike weights for each model in which the predictor was observed divided by the number of models) also provides a measure of relative influence. Standard errors and confidence intervals were calculated from unconditional variance and include model selection uncertainty.

Predictor	Estimate	Standard error [‡]	2.5% CI*	97.5% CI*	I.V
Wetland Count	-0.106	1.2E-01	-3.5E-01	1.4E-01	0.24
Biomass	-0.055	9.4E-02	-2.4E-01	1.3E-01	0.15
Exotic cover	0.0182	5.1E-02	-8.1E-02	1.2E-01	0.15
Mean distance 5	7.3E-03	3.1E-02	-5.3E-02	6.8E-02	0.12
Soil pH	0.029	7.0E-02	-1.1E-01	1.7E-01	0.09
Soil group G %	0.014	4.5E-02	-7.4E-02	1.0E-01	0.11
Peat	-0.016	5.0E-02	-1.1E-01	8.2E-02	0.11
Wetland %	-0.012	4.9E-02	-1.1E-01	8.4E-02	0.06
Intercept	-3.22	3.3E-02	-3.3E+00	-3.2E+00	-
ϕ Intercept[†]	6.86	2.9E-01	6.3E+00	7.4E+00	-

[†]The ϕ intercept is a fitted constant indicating the mean probability of having a non-zero local contribution to β-diversity; [‡] calculated from the unconditional variance (Burnham and Anderson, 2002); * confidence intervals calculated using a normal approximation.

Table 3.7 Pearson correlations between final model set predictors and wetland species richness (see Table 3.1 for description of predictors and Table 3.4 and 3.5 for model selection results). Degrees of freedom in all cases is 24.

Predictor	Pearson's r	t statistic	p-value
biomass	-0.11	-0.54	0.60
exotic cover	0.12	0.61	0.54
soil pH	-0.13	-0.63	0.54
peat	0.08	0.39	0.70
soil type G	-0.27	-1.04	0.17
wetCount	-0.05	-0.24	0.81
ave5	-0.23	-1.15	0.26
pcWet	-0.05	-0.22	0.83

Discussion

Although some caution in interpretation is warranted due to the high number of averaged-model predictors relative to the number of sites, I found support for all three hypotheses influencing wetland plant species composition. Increased competition in wetlands with high biomass resulted in them having similar species composition. As their species richness was unaffected by increased biomass, this suggests they were dominated by a regional pool of competitively superior species rather than monospecific stands. This could indicate that there is adequate niche space available at these wetlands to stabilise any competitive differences among species and maintain their diversity. Niche-based mechanisms also appear to reduce the available species pool; wetlands with widespread permanent inundation and more acidic soil pH conditions had similar species composition, comprising species adapted to these conditions. The role of dispersal—at least at the scale of a few hundred metres—had an unexpected effect, where the uniqueness of wetland plant communities *decreased* as the area and number of different propagule sources increased. If, as I have assumed, the number and area of wetlands is a reliable proxy for propagule diversity and abundance, then recruitment success must be the limiting influence on composition, implying some indirect effect of dispersal probability on wetland invasibility. To verify this however would require an experimental approach.

The niche-based predictors of *peat* and *soil pH* appear to affect species composition through an interaction with the regional species pool (Myers and Harms, 2009). The negative regression coefficient for *peat* (a reliable indicator of permanent saturation) indicates widespread permanent saturation increased community similarity in species composition. Few vascular plant species are adapted to conditions of permanent saturation (Chambers et al., 2008), so communities assemble from a less diverse 'habitat species pool' (Ozinga et al., 2005) in such conditions. The positive regression coefficient for *soil pH*

(indicating acidic conditions were associated with more similar communities of fewer species) was of opposite sign to peat, but represents the same effect. Increases in pH were associated with more unique community composition because wetlands with relatively neutral (higher) pH provide abiotic conditions suited to a wider range of species. Nine wetlands (34 % of total) had soil pH < 5.6, a threshold below which species diversity is reduced to less than one third of the total regional number of species in New York lakes (Weiher and Boylen, 1994). Neither the extent of peat, nor low soil pH, limited species richness within a wetland, but there was less variation in composition among these wetlands because there were fewer species from which the community could assemble. Hence rather than more environmental heterogeneity creating more niche opportunities, harsher conditions impose limits on composition in a habitat, resulting in a filtering effect (Keddy, 1992, Kraft et al., 2015).

In contrast, the positive regression coefficient for *soil type G* indicates wetlands with large areas of this soil type had more unique species compositions. This soil group has a duplex texture with deep sand over clay and is of inherently low fertility (Hall et al., 2009). Infertile soils are associated with high species richness and numbers of rare species in Canadian wetlands (Moore et al., 1989), apparently as a result of reduced biomass and therefore competition. Hence, this result might reflect the influence of decreased competitive pressure along a productivity gradient rather than a niche effect.

The negative regression coefficient for *biomass* indicates increasing competition for resources leads to less unique communities. There was no relationship between wetland species richness and biomass, so it is unlikely the greater similarity was a result of extensive monospecific stands of vegetation (Finlayson et al., 1983, Hocking et al., 1983, Lavergne and Molofsky, 2004). Rather, this result suggests that high biomass wetlands are dominated by a subset of the regional species pool with superior competitive ability, that

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tend to preclude species found at wetlands of lower productivity and biomass. Given this relationship between biomass and species composition, it seems surprising that land use, particularly grazing, was not influential on composition. Livestock grazing can have major effects on the composition of wetland plant communities by removing biomass (e.g., Bakker, 1985, Marty, 2005, Jackson and Allen-Diaz, 2006, Boughton et al., 2010, Jones et al., 2011). Physical disturbance resulting in biomass removal can also increase the probability of immigrating species recruiting by increasing available space and resources (Myers and Harms, 2009). The lack of any land use effect might be a limitation of the data as I had no means to estimate intensity, which greatly affects the outcome of grazing on species composition (Jackson and Allen-Diaz, 2006, Jones et al., 2011). Alternatively, it is possible that grazing sensitive species have been largely removed from these wetlands from past land management.

The largest effect size was associated with an increasing number and area of wetlands within 400 m, which decreased uniqueness. This is the opposite of what I predicted if dispersal limitation largely determined species composition (e.g., Tilman, 1997, Boughton et al., 2010). It was not the composition of the local wetlands that was more similar, but wetlands across the region that occurred in clusters were more similar to each other than those that were more isolated. This was also supported by the small positive effect of increasing mean distance to the nearest five wetlands. Increased short-distance dispersal probabilities from hydrochory could explain increased within-catchment similarity (Chapter 2; Flinn et al., 2010, Nilsson et al., 2010), but this does not explain why clusters of wetlands are less unique in composition at regional scales.

Boughton et al. (2010) observed a sharp decline in species richness in wetlands more than 400-700 m from other wetlands within semi-native pasture in Florida (Boughton et al., 2010), which they interpreted as a dispersal limitation. Dispersal over similar

distances clearly affects wetland plant species composition in this landscape, but I found no evidence of increased species richness in wetlands with many other wetlands in close proximity. Increases in species richness with increasing seed availability can only occur if immigrant species are able to recruit to the community. If increased propagule availability also increased the likelihood that competitively dominant species would reach and colonise a wetland, then competitive exclusion might reduce or prevent recruitment. Thus, an increased probability of competitive dominance could provide one possible explanation for the dispersal-composition pattern I found. This would be analogous to the sampling effect described from studies of the relationship between productivity and biodiversity (Aarssen, 1997, Huston, 1997, Tilman et al., 1997), where as the number of species present increases, so does the probability that one of them will be individually highly productive. Here the effect would represent an increased probability that competitively dominant species would be present at a wetland of higher dispersal and propagule availability.

As with prior studies investigating community assembly processes among wetlands (e.g.,Boughton et al., 2010, Flinn et al., 2010, Douda et al., 2012, Chmara et al., 2013), there appears to be more than one mechanism involved. Despite including estimates of all likely contributing processes, no single mechanism dominates, and there appears to be an interaction between dispersal and competition that depends on the landscape context. This evidence suggests future studies of community assembly in wetlands should avoid tests of any individual process, but rather seek the conditions that determine the ways in which they interact.

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References

AARSSEN, L. W. 1997. High productivity in grassland ecosystems: effected by species diversity or productive species? *Oikos,* 80**,** 183-184.

BAKKER, J. P. 1985. The impact of grazing on plant communities, plant populations and soil conditions on salt marshes. *Vegetatio,* 62**,** 391-398.

BARTON, K. 2014. MuMIn: Multi-Model Inference. R package version 1.12.1.

BORCARD, D. & LEGENDRE, P. 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling,* 153**,** 51-68.

BOUGHTON, E. H., QUINTANA-ASCENCIO, P. F., BOHLEN, P. J., JENKINS, D. G. & PICKERT, R. 2010. Land-use and isolation interact to affect wetland plant assemblages. *Ecography.*

BRAUN-BLANQUET, J. 1932. *Plant sociology: the study of plantcommunities,* New York, NY, US., McGraw-Hill.

BRAY, J. R. & CURTIS, J. T. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs,* 27.

BROCK, M. A. & CASANOVA, M. T. 1997. Plant life at the edges of wetlands: ecological responses to wetting and drying patterns. *In:* KLOMP, N., LUNT, I. (ed.) *Frontiers in Ecology: Building the Links.* Oxford: Elsevier.

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.

BROWN, J. H. 1984. On the relationship between abundance and distribution of species. *American Naturalist,* 124**,** 255-279.

BURNHAM, K. & ANDERSON, D. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach,* New York, Springer.

CALCADA, E. A., CLOSSET-KOPP, D., GALLET-MORON, E., LENOIR, J., REVE, M., HERMY, M. & DECOCQ, G. 2013. Streams are efficient corridors for plant species in forest metacommunities. *Journal of Applied Ecology,* 50**,** 1152-1160.

CASANOVA, M. T. & BROCK, M. A. 2000. How do depth, duration and frequency of flooding influence the establishment of wetland plant communities? *Plant Ecology,* 147**,** 237-250.

CHAMBERS, P. A., LACOUL, P., MURPHY, K. J. & THOMAZ, S. M. 2008. Global diversity of aquatic macrophytes in freshwater. *Hydrobiologia,* 595**,** 9-26.

CHASE, J. M. 2010. Stochastic Community Assembly Causes Higher Biodiversity in More Productive Environments. *Science,* 328**,** 1388-1391.

CHASE, J. M. & MYERS, J. A. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society B-Biological Sciences,* 366**,** 2351-2363.

CHESSON, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics,* 31**,** 343-+.

CHMARA, R., SZMEJA, J. & ULRICH, W. 2013. Patterns of abundance and co-occurrence in aquatic plant communities. *Ecological Research,* 28**,** 387-395.

CONDIT, R., PITMAN, N., LEIGH, E. G., CHAVE, J., TERBORGH, J., FOSTER, R. B., NUNEZ, P., AGUILAR, S., VALENCIA, R., VILLA, G., MULLER-LANDAU, H. C., LOSOS, E. & HUBBELL, S. P. 2002. Beta-diversity in tropical forest trees. *Science,* 295**,** 666-669.

CONNOR, E. F. & MCCOY, E. D. 1979. Statistics and biology of the species-area relationship. *American Naturalist,* 113**,** 791-833.

COTTENIE, K. 2005. Integrating environmental and spatial processes in ecological community dynamics. *Ecology Letters,* 8**,** 1175-1182.

CRIBARI-NETO, F. & ZEILEIS, A. 2010. Beta Regression in R. *Journal of Statistical Software,* 34**,** 1-24.

DOUDA, J., DOUDOVA-KOCHANKOVA, J., BOUBLIK, K. & DRASNAROVA, A. 2012. Plant species coexistence at local scale in temperate swamp forest: test of habitat heterogeneity hypothesis. *Oecologia,* 169**,** 523-534.

FERRARI, S. L. P. & CRIBARI-NETO, F. 2004. Beta regression for modelling rates and proportions. *Journal of Applied Statistics,* 31**,** 799-815.

FINLAYSON, C. M., ROBERTS, J., CHICK, A. J. & SALE, P. J. M. 1983. The biology of Australian weeds : 11. Typha domingensis Pers. and Typha orientalis Presl. *Journal - Australian Institute of Agricultural Science,* 49**,** 3-10.

FLINN, K. M., GOUHIER, T. C., LECHOWICZ, M. J. & WATERWAY, M. J. 2010. The role of dispersal in shaping plant community composition of wetlands within an old-growth forest. *Journal of Ecology,* 98**,** 1292-1299.

FREESTONE, A. L. & INOUYE, B. D. 2006. Dispersal limitation and environmental heterogeneity shape scale-dependent diversity patterns in plant communities. *Ecology,* 87**,** 2425-2432.

GELMAN, A. 2008. Scaling regression inputs by dividing by two standard deviations. *Statistics in Medicine,* 27**,** 2865-2873.

GELMAN, A. & SU, Y. 2015. arm: Data Analysis Using Regression and Multilevel/Hierarchical Models. R package version 1.8-6 ed.

GOTELLI, N. J. & COLWELL, R. K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters,* 4**,** 379-391.

GRACE, J. B. & WETZEL, R. G. 1981. Habitat partitioning and competitive displacement in cattails (Typha) - experimental field studies. *American Naturalist,* 118**,** 463-474.

GRUEBER, C. E., NAKAGAWA, S., LAWS, R. J. & JAMIESON, I. G. 2011. Multimodel inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology,* 24**,** 699-711.

HALL, J. A. S., MASCHMEDT, D. J. & BILLING, N. B. 2009. *The soils of southern South Australia,* Adelaide, Department of Water, Land and Biodiversity Conservation.

HILLE RIS LAMBERS, J., ADLER, P. B., HARPOLE, W. S., LEVINE, J. M. & MAYFIELD, M. M. 2012. Rethinking Community Assembly through the Lens of Coexistence Theory. *In:* FUTUYMA, D. J. (ed.) *Annual Review of Ecology, Evolution, and Systematics, Vol 43.*

HOCKING, P. J., FINLAYSON, C. M. & CHICK, A. J. 1983. The biology of Australian weeds. 12. Phragmites australis (Cav.) Trin. ex Steud. *Journal - Australian Institute of Agricultural Science,* 49**,** 123-132.

HUBBELL, S. P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography, Monographs in Population Biology,* Princeton, Princeton University Press.

HURTT, G. C. & PACALA, S. W. 1995. The consequences of recruitment limitation - reconciling chance, history and competitive differences bewteen plants. *Journal of Theoretical Biology,* 176**,** 1-12.

HUSTON, M. A. 1997. Hidden treatments in ecological experiments: Re-evaluating the ecosystem function of biodiversity. *Oecologia,* 110**,** 449-460.

HUTCHINSON, G. E. 1957. Concluding remarks. *Cold Spring Harbor Symposium on Quantitative Biology,* 22**,** 415-427.

JACKSON, R. D. & ALLEN-DIAZ, B. 2006. Spring-fed wetland and riparian plant communities respond differently to altered grazing intensity. *Journal of Applied Ecology,* 43**,** 485-498.

JONES, W. M., FRASER, L. H. & CURTIS, P. J. 2011. Plant community functional shifts in response to livestock grazing in intermountain depressional wetlands in British Columbia, Canada. *Biological Conservation,* 144**,** 511-517.

KEDDY, P. A. 1992. Assembly and response rules - 2 goals for predictive community ecology. *Journal of Vegetation Science,* 3**,** 157-164.

KOLEFF, P., GASTON, K. J. & LENNON, J. J. 2003. Measuring beta diversity for presence-absence data. *Journal of Animal Ecology,* 72**,** 367-382.

KRAFT, N. J. B., ADLER, P. B., GODOY, O., JAMES, E. C., FULLER, S. & LEVINE, J. M. 2015. Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology,* 29**,** 592-599.

LAVERGNE, S. & MOLOFSKY, J. 2004. Reed canary grass (Phalaris arundinacea) as a biological model in the study of plant invasions. *Critical Reviews in Plant Sciences,* 23**,** 415-429.

LEGENDRE, P. 2014. Interpreting the replacement and richness difference components of beta diversity. *Global Ecology and Biogeography,* 23**,** 1324-1334.

LEGENDRE, P. & DE CACERES, M. 2013. Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. *Ecology Letters,* 16**,** 951-963.

LEIBOLD, M. A. 1995. The niche concept revisited - mechanistic models and community context. *Ecology,* 76**,** 1371-1382.

LEIBOLD, M. A., HOLYOAK, M., MOUQUET, N., AMARASEKARE, P., CHASE, J. M., HOOPES, M. F., HOLT, R. D., SHURIN, J. B., LAW, R., TILMAN, D.,

LOREAU, M. & GONZALEZ, A. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters,* 7**,** 601-613.

LENSSEN, J., MENTING, F., VAN DER PUTTEN, W. H. & BLOM, K. 1999. Control of plant species richness and zonation of functional groups along a freshwater flooding gradient. *Oikos,* 86**,** 523-534.

MACARTHUR, R. & LEVINS, R. 1967. Limiting similarity convergence and divergence of coexisting species. *American Naturalist,* 101**,** 377-+.

MACARTHUR, R. & WILSON, E. 1967. *The theory of island biogeography,* Princeton, NJ, Princeton University Press.

MARTY, J. T. 2005. Effects of Cattle Grazing on Diversity in Ephemeral Wetlands. *Conservation Biology,* 19**,** 1626-1632.

MOORE, D. R. J., KEDDY, P. A., GAUDET, C. L. & WISHEU, I. C. 1989. Consevation of wetlands - do infertile wetlands deserve a higher priority. *Biological Conservation,* 47**,** 203-217.

MYERS, J. A. & HARMS, K. E. 2009. Seed arrival, ecological filters, and plant species richness: a meta-analysis. *Ecology Letters,* 12**,** 1250-1260.

NAKAGAWA, S. & FRECKLETON, R. P. 2011. Model averaging, missing data and multiple imputation: a case study for behavioural ecology. *Behavioral Ecology and Sociobiology,* 65**,** 103-116.

NILSSON, C., BROWN, R. L., JANSSON, R. & MERRITT, D. M. 2010. The role of hydrochory in structuring riparian and wetland vegetation. *Biological Reviews,* 85**,** 837-858.

O'CONNELL, J. L., JOHNSON, L. A., BEAS, B. J., SMITH, L. M., MCMURRY, S. T. & HAUKOS, D. A. 2013. Predicting dispersal-limitation in plants: Optimizing

planting decisions for isolated wetland restoration in agricultural landscapes. *Biological Conservation,* 159**,** 343-354.

OKSANEN, J., GUILLAUME BLANCHET, F., KINDT, R., LEGENDRE, P., MINCHIN, P., O'HARA, R., SIMPSON, G., SOLYMOS, P., STEVENS, H. & WAGNER, H. 2013. vegan: Community Ecology Package. R package version 2.0-10.

OZINGA, W. A., SCHAMINEE, J. H. J., BEKKER, R. M., BONN, S., POSCHLOD, P., TACKENBERG, O., BAKKER, J. & VAN GROENENDAEL, J. M. 2005. Predictability of plant species composition from environmental conditions is constrained by dispersal limitation. *Oikos,* 108**,** 555-561.

PEINTINGER, M., BERGAMINI, A. & SCHMID, B. 2003. Species-area relationships and nestedness of four taxonomic groups in fragmented wetlands. *Basic and Applied Ecology,* 4**,** 385-394.

R CORE TEAM 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

SANTAMARIA, L. 2002. Why are most aquatic plants widely distributed? Dispersal, clonal growth and small-scale heterogeneity in a stressful environment. *Acta Oecologica-International Journal of Ecology,* 23**,** 137-154.

SASAKI, T., KATABUCHI, M., KAMIYAMA, C., SHIMAZAKI, M., NAKASHIZUKA, T. & HIKOSAKA, K. 2012. Diversity partitioning of moorland plant communities across hierarchical spatial scales. *Biodiversity and Conservation,* 21**,** 1577-1588.

SHI, J., MA, K., WANG, J., ZHAO, J. & HE, K. 2010. Vascular plant species richness on wetland remnants is determined by both area and habitat heterogeneity. *Biodiversity and Conservation,* 19**,** 1279-1295.

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SHI, J. M., MA, K. M., WANG, J. F., ZHANG, Y. X. & ZHAO, J. Z. 2013. Determinants of plant species-richness in different wetland types along a hydrological gradient: implications for conservation. *Polish Journal of Ecology,* 61**,** 645-654.

SILVERTOWN, J., DODD, M. E., GOWING, D. J. G. & MOUNTFORD, J. O. 1999. Hydrologically defined niches reveal a basis for species richness in plant communities. *Nature,* 400**,** 61-63.

SIMAS, A. B., BARRETO-SOUZA, W. & ROCHA, A. V. 2010. Improved Estimators for a General Class of Beta Regression Models. *Computational Statistics & Data Analysis,* 54**,** 348–366.

STEVENS, A. 2006. Fleurieu Peninsula Swamp Vegetation Survey 2006 Floristic Definition of the Fleurieu Peninsula Swamps. Adelaide.

THOMAZ, S. M., SOUZA, D. C. & BINI, L. M. 2003. Species richness and beta diversity of aquatic macrophytes in a large subtropical reservoir (Itaipu Reservoir, Brazil): the influence of limnology and morphometry. *Hydrobiologia,* 505**,** 119-128.

TILMAN, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology,* 78**,** 81-92.

TILMAN, D., LEHMAN, C. L. & THOMSON, K. T. 1997. Plant diversity and ecosystem productivity: Theoretical considerations. *Proceedings of the National Academy of Sciences of the United States of America,* 94**,** 1857-1861.

TUOMISTO, H. 2010. A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography,* 33**,** 2-22.

TUOMISTO, H., RUOKOLAINEN, K. & YLI-HALLA, M. 2003. Dispersal, environment, and floristic variation of western Amazonian forests. *Science,* 299**,** 241-244.

VELLEND, M. 2010. Conceptual synthesis in community ecology. *Quarterly Review of Biology,* 85**,** 183-206.

WEIHER, E. & BOYLEN, C. W. 1994. Patterns and prediction of alpha and beta diversity of aquatic plants in adirondack (New York) lakes. *Canadian Journal of Botany,* 72**,** 1797-1804.

WHITTAKER, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs,* 30**,** 280-338.

WICKHAM, H. 2009. *ggplot2: elegant graphics for data analysis,* New York, Springer

ZEDLER, J. B. & KERCHER, S. 2004. Causes and consequences of invasive plants in wetlands: Opportunities, opportunists, and outcomes. *Critical Reviews in Plant Sciences,* 23**,** 431-452.

Statement of authorship Chapter 4

Chapter 4   Future extinction risk for wetland plants is higher from individual patch loss than total area reduction

Abstract

Quantifying the risk of extinction due to habitat loss is an increasingly urgent task for the design and implementation of effective conservation interventions. Methods based on species- and endemics-area relationships are well developed, but applications to date have concentrated primarily on the fragmentation of formerly continuous habitats such as forests and woodlands. Extinction risk due to area loss in habitat types occurring naturally as spatially discrete patches has been largely ignored. I address this knowledge gap, using a network of seasonally connected wetlands to illustrate my approach. I modelled the risk of extinction associated with wetland native plant communities under two alternative scenarios: the loss of (*i*) entire wetlands (*patch loss*) versus (*ii*) an equivalent area while retaining total wetland number (*area loss*). Patch loss scenarios resulted in an average of 72 % more species going extinct than the equivalent area loss. Extinction due to patch loss was highest when wetlands were removed in increasing size order (smallest to largest) – a plausible scenario arising from projected climatic drying in the region. For area loss, direct clearance of ecotones presents a higher extinction risk than reductions in hydrological niche breadth due to the large number of terrestrial species found within wetland fringes. Extinction risk associated with naturally occurring habitat patches depends on the distribution of regionally endemic species; where this is not a function of habitat area, loss of individual small patches presents higher risk than an equivalent reduction in total habitat area across the network.

Introduction

Habitat reduction and fragmentation have long been identified as factors increasing species'

extinction risk (e.g. Ehrlich and Ehrlich, 1981), so quantifying the relationship between

area and species loss has been an important tool for conservation planning. The simplest

and most common approach for predicting change in species number from habitat loss or

fragmentation is the species-area relationship, where the expected *equilibrium* number of

species decays non-linearly with declining total habitat area (e.g. Pimm and Askins, 1995,

Brooks et al., 1997). Using species-area relationships to predict extinction has, however,

been controversial (reviewed in Halley et al., 2013), in part due to their tendency to over-

predict the number of species at risk (Heywood et al., 1994, May et al., 1995). These

overestimates have been shown to likely arise from a sampling artefact when the species-

area relationship is used to predict the area required to remove all individuals of a species

(He and Hubbell, 2011). This over-estimation can be avoided by instead predicting

extinction using the endemics-area relationship (He and Hubbell, 2011, He and Hubbell,

2013), an approach introduced by Harte and Kinzig (1997).

Endemic species are those occurring over limited geographical areas (Harte and

Kinzig, 1997, Kinzig and Harte, 2000) and this limited spatial distribution generally places

them at higher extinction risk than those with broader distributions (Sodhi et al., 2009). As

a result, protecting the most species-rich sites does not necessarily achieve the lowest

extinction rate because sites with the highest species richness do not always have high

endemicity (Prendergast et al., 1993, Zurlini et al., 2002). Therefore, considering the spatial

distribution of endemics is important for conservation planning (Rodrigues and Gaston,

2001), including the prediction of extinction risk. Although the term 'endemic' commonly

refers to global distributions, it can also be applied to distinguish 'species found only in a

sub-patch of a larger distinct biome' (Harte and Kinzig, 1997; p. 419).

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A common theme in extinction studies using species- or endemics-area methods is a focus on patches that remain after the fragmentation of a formerly continuous habitat area. Examples include temperate woodlands (Pimm and Askins, 1995) or tropical forests (Brook et al., 2003), with studies typically evaluating risk at continental or larger scales (e.g. Ulrich, 2005, Malcolm et al., 2006). The use of species-area based methods to predict extinction patterns on true islands also has some validation (e.g. Brooks et al., 1997, Gibson et al., 2013), but there has been no attempt to apply these methods to their habitat-island analogues: ecosystems that occur naturally as discrete patches in a contrasting and largely hostile matrix. Many such systems (e.g., wetlands or coral reefs) support high biodiversity and are losing both area and entire patches, but the use of species- or endemics-area based methods in this context has not yet been investigated. I address this gap, applying the endemics-area relationship to determine the extinction risk arising from habitat loss for a network of discrete wetland patches.

Understanding the consequences of reduced wetland area for biodiversity is necessary; global wetland area has already been reduced to between 29 and 36 % of what it was just over a century ago, declining on average at a rate of > 1 % year^{-1}, with annual losses of up to 2 % in Asia and the Neotropics (Davidson, 2014). These rates of loss currently show no signs of slowing (Davidson, 2014) and are similar to the estimated 1.4 % loss of humid tropical forest occurring between 2000 and 2005 (Hansen et al., 2008). The high diversity and endemicity of freshwater biota (Dudgeon et al., 2006, Balian et al., 2008) suggests that many wetland species are likely to have been extirpated. While there have been studies quantifying the risk of habitat loss for freshwater fish (Xenopoulos and Lodge, 2006, Giam et al., 2011, 2012) and riparian vegetation (Ström et al., 2012), the effect of area loss on wetland plant communities at regional or larger scales has not been quantified.

I modelled the risk of extinction for wetland plants in a typical (temperate) agricultural landscape, comparing the loss of entire patches with the equivalent area spread evenly across wetlands, the latter estimated using an endemics-area based approach. My a priori hypothesis is that wetland patch loss will cause a higher extinction risk because of high β-diversity and the many rare terrestrial species found in the study region (Chapter 2). I show that loss of entire wetland patches not only leads to a higher extinction risk compared to an equivalent reduction in area, but the loss of smaller wetlands creates the highest risk of species extinctions for any amount of area loss.

Methods

My study region was the Fleurieu Peninsula in South Australia, covering an area of 1200 km^2 centred approximately on latitude 35.5 °S. The climate of the region is Mediterranean with warm, dry summers and cool wet winters. Rainfall varies from 500 – 900 mm/yr and predominantly falls during winter-spring months. I obtained a regional vegetation survey dataset described in Stevens (2006), to which I added vegetation survey data from a state agency database, selecting only wetlands with near-complete censuses as described in Chapter 2. I removed exotic plants from the analysis, but retained terrestrial species. The final dataset included 34 wetlands ranging in size from 0.63 – 38.6 ha, with native plant species richness ranging from 14 to 84/wetland. Total native plant species richness was 163 species. To provide a more general result, I converted both richness and area to proportions of total values.

Patch loss: loss of entire wetlands

To estimate extinction loss following the removal of entire individual wetlands within the network, I removed wetlands individually and calculated the number of endemic species that were restricted to those removed. My analysis assumes that patch loss will result in

conversion to agriculture and loss of all native species (e.g. wetland conversion for row crop expansion in the U.S.; Johnston, 2013). I use a random patch-loss model as a point of comparison for other patch- and area-loss scenarios. Here I removed a single wetland at a time and calculated the number of extinct species that arise across the study region, then iteratively resampling the matrix 100 times without replacement and repeating the procedure. I repeated this process, removing two randomly selected wetlands at a time, continuing these calculations up to to $n - 1$ wetlands.

I also removed wetlands following three specific orderings of the data according to wetland size and proximity, quantifying extinction as the number of species found only in the wetlands removed. I estimated uncertainty (95 % confidence limits) in extinction rates using a bootstrapping procedure, randomly resampling wetland communities with replacement and re-calculating the expected value over 1000 simulations. I removed wetlands according to three patch-loss scenarios:

(1) *Increasing size order* (smallest wetland lost first, remainder removed in increasing size order): in my study region, most wetlands form on 'perched' aquifers — small groundwater lenses of limited storage capacity and highly dependent on reliable winter-spring rainfall to maintain saturation. Smaller wetlands reflect smaller perched aquifers and I consider these wetlands to be the most exposed to losses resulting from reduced annual rainfall. Smaller wetlands are also more susceptible to other terrestrialisation risks associated with wetland loss, such as sedimentation (Johnson et al., 2012).

(2) *Decreasing size order* (largest wetlands lost first): initial loss of large wetlands could arise for two main reasons: (*i*) The largest wetlands tend to be dependent on large regional groundwater systems, which are subject to human extraction; therefore, removing large wetlands first replicates excessive human extraction of groundwater.

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(*ii*) This scenario also replicates the transformation of large wetlands to productive land via direct drainage, whereby larger wetlands are targeted because of the increased area returned per investment. Although current environmental policies prevent this in my study region, wetland conversion for agriculture still occurs in developed countries (e.g. Johnston, 2013) and remains a plausible scenario in developing parts of the world such as Asia and the Neotropics where the highest rates of wetland loss occur (Davidson, 2014).

(3) *Distance* (closest wetlands removed first): Starting at randomly selected focal point and removing the nearest wetlands first, I tested for a difference in local versus regional distributions. This reflects a possible scenario where wetlands within a large contiguous area were lost due to broad-scale land use conversion, for example plantation forest establishment (Dahl, 2011). If neighbouring wetlands tended to have similar species compositions, this might reduce the overall reduction in the regional species pool associated with removing clusters of wetlands. This should be evident by the species loss curve for wetlands ordered by proximity falling below the random wetland loss.

Area loss: decreases in wetland area, but not number

To predict within-wetland species loss I required data describing the spatial distribution of endemic species and I used an empirical approach. Database surveys provided estimates of total wetland species richness and identities, but because quadrats were not connected, they confound α- and β-diversity (Smith, 2010) and could not be used to estimate the endemics-area relationship. To build an empirical intra-wetland endemics-area curve, I instead collected data from four continuous grids consisting of 100 ten-m^2 cells in a 10 row $\times$ 10 column configuration. Grids were located within four contrasting vegetation types across a water-availability gradient to represent the range of intra-wetland variability in the spatial

distribution of species. For each grid I calculated an empirical endemics-area curve by sampling areas of increasing size, following a similar method to that described in He and Hubbell (2011). This involved iteratively resampling the grid with an increasing size-sampling window and calculating the mean number of species confined only to the window for each size increment. That is, I first calculated the average number of species found only in a single grid square, with this representing the endemic species at 10-m^2 scale. I then increased the sampling window up to plot scale to obtain four endemics-area relationships, averaging the resulting curves across the four grids to obtain my final model. I used a similar method to estimate the species-area relationship.

He and Hubbell (2011) provide an equation for the power-law endemics-area relationship:

$$S_{loss}/S_A = 1 - (1 - a/A)^{z'} \tag{1}$$

where S_{loss}/S_A is the fraction of species lost, a/A is the fraction of area remaining and z' is a fitted slope parameter and is generally $< z$ estimated from the power-law species-area relationship built from the same data (He and Hubbell, 2011). I fitted equation 1 to the mean of my empirical average endemics-area relationship and used this model to predict the number of species lost for a given decrease in intra-wetland area. I used the value predicted by the upper 95 % confidence bound for the mean slope parameter as a conservative (worst-case) inference of extinction risk. I also fitted a power-law species-area curve to the same dataset. Both equation 1 and the power-law species-area curve were fitted using non-linear least squares analysis in the R programming language (R Core Team, 2014).

The intra-wetland empirical endemics-area relationship provides an estimate of the proportion of species likely to be removed from a wetland for a given decrease in area. To then determine how many species would be lost at regional scale, I sampled the number of

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species predicted by equation 1 to be lost from each wetland, then calculated how many endemics this represented at a regional scale. Repeating this procedure 1000 times provided a distribution of regional extinctions for a given area of wetland loss (species), allowing direct comparisons with the wetland patch-loss predictions (see below).

Extinction risk is generally thought to be inversely proportional to occupancy at regional scale and to abundance at local (wetland) scale; lower values of either variable increases that species' extinction risk. The effects of occupancy are dealt with explicitly in the model, but to set sampling probabilities I required an estimate of how much wetland-scale abundances vary from species-to-species. It is also well known that species local abundance and regional occupancy tend to be positively correlated. With the exception of the null model, which used random sampling (all species had equal probability of being removed) I set each species sampling probability to be inversely proportional to its occupancy as a proxy measure of local abundance. Finally, the probability of extinction at a site is likely to differ among species under different area-loss mechanisms. I addressed this by varying the sampling probability for each species, comparing the relative change in extinction risk according to two plausible (but essentially arbitrary) mechanisms of wetland loss/degradation, a worst-case scenario and a random-loss null model:

Hydrology Scenario: hydrology is the major determinant of wetland plant zonation (Grace and Wetzel, 1981, Brock and Casanova, 1997) and permanent drying is the most likely process leading to area loss in these seasonal wetlands. To simulate this, I applied a hydrological classification to assign the relative probability of a wetland species being removed. I used the plant functional group designation of Casanova (2011) to assign an increased probability of selection for functional groups that require deep water and long inundation periods (i.e., submerged, then amphibious plants).

Agricultural Encroachment Scenario: where wetland fringes are progressively brought under productive use, possibly concurrent with more gradual drying. This scenario would most likely cause the loss of fringing ecotone species of low requirement for inundation. To simulate this, I sampled terrestrial species (functional groups 'Tdry' and 'Tdamp') at twice that of amphibious and submerged species.

Endemic Species Loss (Worst Case) Scenario: where endemic species were preferentially removed. This represents the worst-case situation, where the rarest species were assigned the highest sampling probabilities. Endemic species (here defined as species occurring in only one wetland) were assigned twice the sampling probability of more widespread species.

Random sampling: as a null model I assigned equal sampling probabilities to all species.

Comparing patch- and area-loss scenarios

I compared the consequences of wetland patch- and area-loss scenarios against a null model with random wetland patch loss. I removed different numbers of randomly chosen wetland patches, calculating the total resulting area loss as a fraction of the total wetland area. I then removed the equivalent proportion of wetland area from each individual wetland patch and estimated regional species loss following the procedure described above. I compared estimated species loss for my two habitat-reduction scenarios against the null models for area loss levels of 20, 40, 50, 60 and 80 %.

Results

For a given loss of total regional wetland area, species extinctions as a result of patch loss were always higher when smaller wetlands were removed first (Fig. 4.1). Removing

wetlands in order of decreasing size resulted in fewer extinctions for a given area than did random selection (Fig. 4.1). There was no evidence that the number of endemic species was correlated with wetland area (Kendall's $\tau = 0.03$, $n = 34$, $p = 0.44$), or total species richness (Kendall's $\tau = 0.16$, $n = 34$, $p = 0.11$). The random-removal patch loss scenario predicts the extinction of around one quarter of the regional species pool (mean [95 % confidence limits] = 21.8 [15.6, 27.8] %) for a 50 % loss of regional wetland area. The distance-based results closely follow the random removal pattern up to about 50 % area loss, above which extinction rises more rapidly for the distance-based calculation (Fig. 4.2).
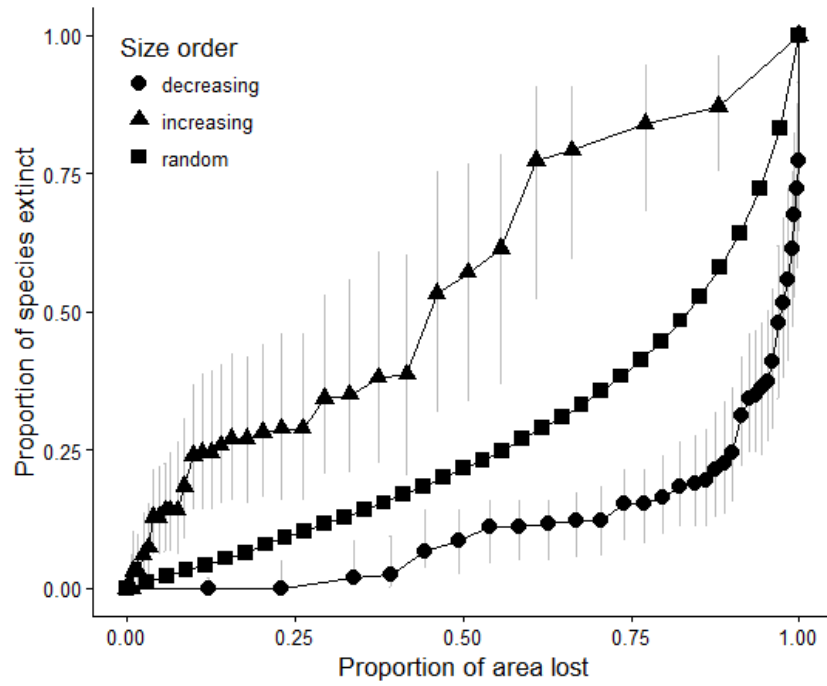
Figure 4.1 Predicted proportion of regional species extinctions as entire wetlands are removed. The *x*-axis shows the proportion of total wetland area that is accounted for as individual wetlands are removed based on three different orderings: decreasing (circles) and increasing (triangles) size order, and random selection (squares). Grey lines are bootstrapped 95% confidence intervals, shown only for the decreasing and increasing response for clarity.
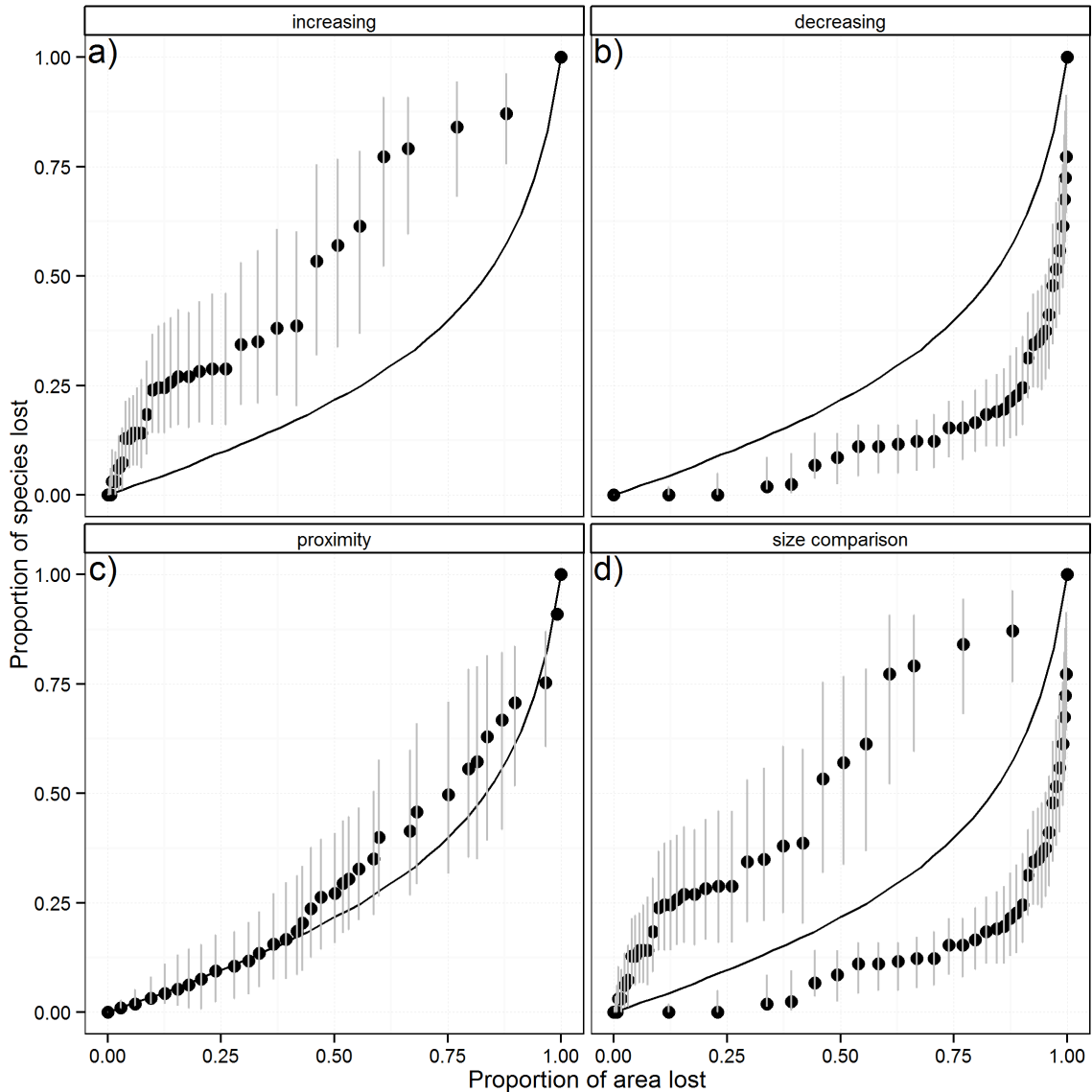
Figure 4.2 Comparison of patch loss scenarios. Each point represents the proportion of the regional species pool that is lost (*y*-axis) for the loss of the total area shown on the *x*-axis. Values were calculated by removing individual wetlands sequentially according to different ordering of the data. So viewing panel a) from left to right, the first point shows the proportion of species lost when the smallest patch is removed; the second point shows the proportion lost when the two smallest wetlands are both removed and so on. Each panel compares the estimated lost proportion for the relevant size ordering to a random loss indicated by the continuous curve. In panels a-c different orderings of the data are compared and panel d plots the ordering shown in panels a and b on a common axis for comparison (see also Fig.4.1). The distance-based scenario described in the main text is shown in panel c (headed 'proximity'). In all cases grey vertical lines represent 95% bootstrapped confidence intervals.

The power-law endemics-area relationship (equation 1) and the power-law species-area relationship fit the data well (coefficient of determination R^2 for both models > 0.99), passing within the range of empirical measurement uncertainty (95 % confidence limits)

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over all area values. The slope (z) for the power-law endemics-area relationship $z = 0.13$ [0.11, 0.15] (mean and 95% confidence limits) was smaller than that of the power-law species-area relationship ($z = 0.19$ [0.18, 0.21]). The upper 95 % uncertainty limits of z for the power-law endemics-area curve encompasses the empirical variability for positive values up to 80 % area loss, but the lower limit does not capture the full range of negative measurement error (Fig. 4.3). At the wetland scale, a loss of 50 % of area is predicted to result in 9 [3.8, 12.8] % (mean [± 95 % confidence limits]) of species going extinct from that wetland (Fig. 4.4).
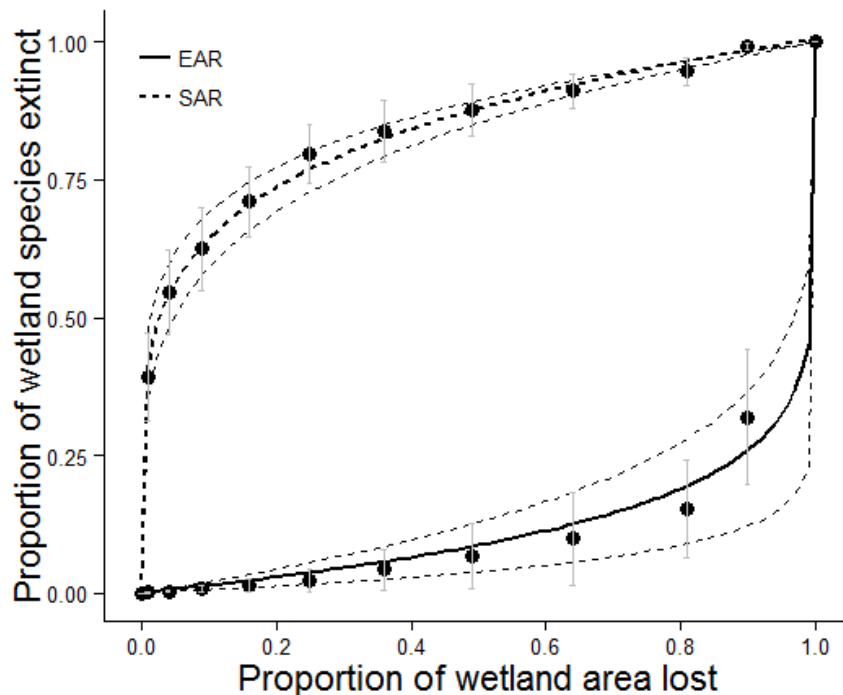
Figure 4.3 Predicted extinctions for a given loss of area within a single wetland. The endemics-area (lower curve) and species-area (upper curve) relationships are modelled using equation 1 ($z = 0.13$) and the power function species-area relationship ($z = 0.19$), respectively. Grey lines are 95% confidence intervals based on four sampling grids of 100 cells each. Dashed lines show curves fitted using 95 % uncertainty bounds of z.

The highest loss of regional species for area-based scenarios was when endemic species were removed preferentially, but the ecotone-loss scenario predicted only slightly

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fewer losses, and 95 % confidence limits overlapped up to a 80 % area loss (Fig. 4.5). The

hydrological scenario resulted in relatively lower extinction risk for all area losses and the

relative differences increased the larger the area lost (Fig. 4.5). Losing 50 % of wetland

area predicted 10 % of species to disappear from each wetland, which translates to < 7 % of

species in the regional pool (Fig. 4.5).
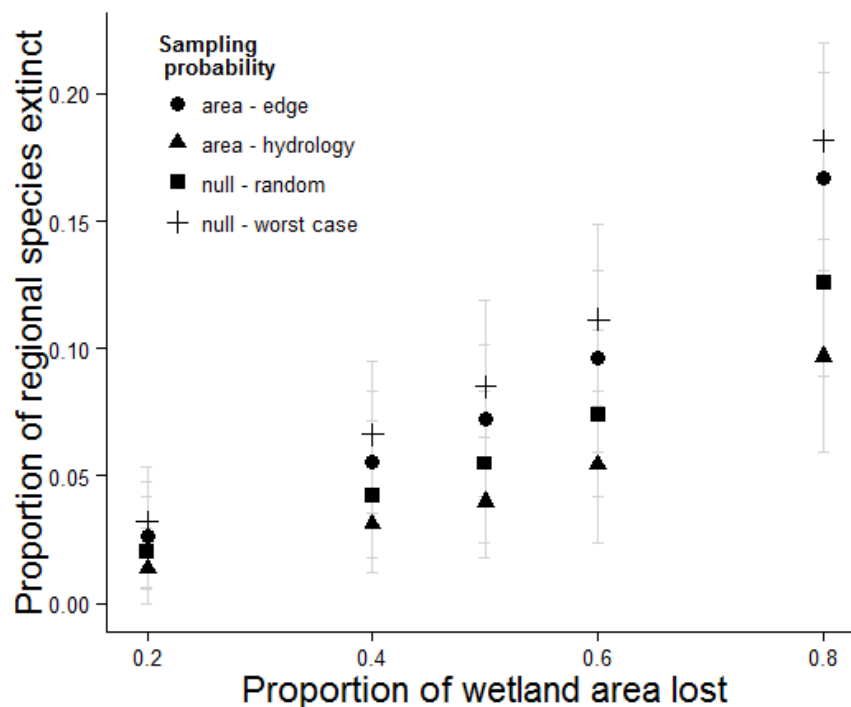
Figure 4.4 Regional proportional loss of species predicted from a given proportional loss of
area at each of the wetlands in the network for the four sampling probabilities. If all
wetlands lost the proportion of area shown on the *x*-axis (evaluated at 20, 40, 50, 60 and 80
%), the regional loss of species predicted is shown on the *y*-axis.

For all wetland area loss scenarios, fewer species extinctions are predicted than for

random patch loss (Fig. 4.5). Based on the worst case area loss scenario, mean expected

species extinctions are consistently close to one third of those predicted under patch loss

across all reductions in total area (range 33.2-36.3%). Comparing the lower and upper 95 %

confidence limits for patch and area loss predictions respectively, the difference between

the two mechanisms averaged 33.7 %, but increased monotonically with total area (range

11.7 – 50.4 %, Fig. 4.5).
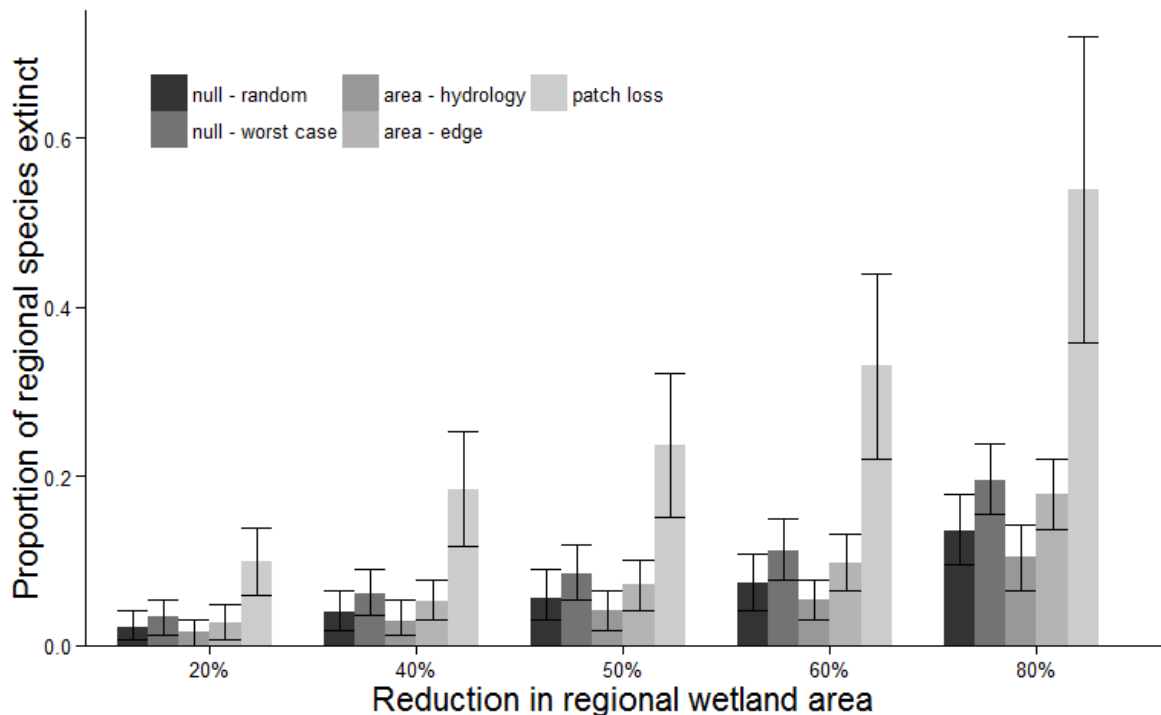
Figure 4.5 Comparison of species predicted to become extinct when wetlands are removed (patch loss) or decreased in size (area loss). Each set of comparisons represents the random patch-loss estimate and four area-loss estimates: 'area – hydrology' preferentially removes species requiring longer periods of inundation and simulates the effects of climatic drying; 'area - edge' preferentially removes species found in wetland fringes simulating agricultural encroachment into wetland fringes. Two null models provide points of reference 'null – worst case' preferentially samples endemic species; 'null – random' samples species totally at random. The *x*-axis shows the percentage of wetland area lost. Mean species loss is indicated by the height of the bars, while error bars show 95% confidence intervals obtained using 1000 simulations (calculating using bootstrapping for patch-loss scenarios and resampling under the relevant species sampling probabilities for the area loss scenarios).

Discussion

Removing entire wetlands results in a higher risk of plant extinctions compared to the loss

of an equivalent area of habitat spread evenly across the network of wetlands. Losing

smaller wetland patches leads to more regional species extinctions for a given proportion of

area lost. Among the area-based scenarios, agricultural encroachment into wetland fringes, which disproportionately impacts ecotone diversity, would result in the greatest reduction in regional species richness within Fleurieu wetlands.

I found that the total number of species accumulated more rapidly from small to large habitat (wetland) patches, which has also been shown for calcareous fens (Peintinger et al., 2003) and terrestrial forest fragments (Honnay et al., 1999). I also found that the number of endemic species was not related to wetland size — Simberloff and Gotelli (1984) found that smaller prairie and forest remnants in the American mid-west had *more* rare species than expected under a random colonisation model due to their higher-than-expected species richness. A possible explanation for this in Fleurieu wetlands is a passive sampling effect (Connor and McCoy, 1979) due to the larger perimeter-to-area (and therefore also edge-to-interior) ratio in small wetlands. Colonization opportunities within this proportionally larger edge zone would be greater due to the increased physical disturbance resulting in higher species turnover that could also counter competitive dominance. The important contribution to total species richness made by small and large wetland patches supports prior calls to conserve habitat patches of all sizes to maintain regional biodiversity (Scheffer et al., 2006, Davies et al., 2008, Della Bella et al., 2008, Maltchik et al., 2010). Protection of the largest or most species-rich patches in this heavily cleared landscape would not guarantee the lowest extinction risk.

Seasonal wetlands of temperate climatic zones such as those in my study region are among some of the most threatened habitats (Holland et al., 1995), but can have species-rich ecotones that include native terrestrial species (Haukos and Smith, 1994, Brock and Casanova, 1997, Brose, 2001, Flinn et al., 2008, Kaeser and Kirkman, 2009). Fleurieu wetlands have high β-diversity mostly driven by ecotone species (Chapter 2). I show the loss of these ecotone species from edge effects, such as via agricultural encroachment,

causes a greater extinction risk compared to a reduction in the hydrological gradient. This result should not be interpreted to indicate that drying presents a relatively low risk to wetland biodiversity. Plant species richness is only one measure of wetland biodiversity and both aquatic flora and fauna would clearly be adversely affected by any permanent reduction in water availability. Changes to hydrology is a serious threat to these wetlands, with downscaled climate projections for the region suggesting declining annual rainfall and increasing temperatures (Charles and Fu, 2014). The resulting changes in catchment water balance will mean that smaller wetlands with a reduced storage volume to buffer drought periods will be at risk of drying completely, with conversion to agricultural land use a likely outcome. Based on my modelling, such losses could result in many extinctions within wetlands in the region.

Prior to my study, few have predicted wetland plant species loss under global change scenarios. Rare exceptions include Rosset et al. (2010), who used generalised additive models to predict the species richness of different taxonomic groups in Swiss ponds based on projected temperature and related water-quality changes, but reported only pond-scale changes in richness. Ström et al. (2012) used changes in inundation patterns forecasted under climate projections to predict corresponding changes in the species richness of riparian vegetation associations. Their study was based on changes in zone width, not area, and makes only a qualitative estimate of overall species change. Other studies have predicted wetland area loss, but have made no attempt to quantify the biological consequences (e.g. Poiani and Johnson, 1993, Alahuhta et al., 2011, Essl et al., 2012). My method provides both regional estimates of species loss and avoids any scale-related sampling issues by using nested samples and employing endemics-area relationships. The approach can be readily integrated with explicit predictions of change in habitat area, for example from hydrological models, and also provides a flexible means to

incorporate information on species spatial distributions. Sampling probabilities can be modified to reflect differential species exposure to area-loss mechanisms using traits or other autecological knowledge.

My use of a generalised endemics-area relationship collated across multiple grids is a novel approach, but it introduces some uncertainty in the predictions arising. I accounted for this by adopting a worst-case estimate based on the upper 95 % confidence limit of predicted wetland-scale species loss. There are few points of comparison to validate my parameter estimates for the endemics-area relationship due to a lack of published empirical values (Smith, 2010). He and Hubbell (2011) report a range of empirical values for 50-ha forest sites across a climatic gradient at $z' = 0.065$ to 0.126 (95 % confidence limits; mean = 0.097; $n = 8$). My mean z' of 0.131 just exceeds their upper confidence limit, but until more wetland estimates become available it is difficult to place this value in a broader context.

Using species- or endemics-area relationships to predict extinction risk remains controversial and both methods have attracted criticism (e.g. Ibanez et al., 2006, He and Hubbell, 2011, He and Hubbell, 2012, Pereira et al., 2012, Halley et al., 2013, Rybicki and Hanski, 2013). Endemics-area based extinction estimates provide the best estimate of *immediate* extinction (He and Hubbell, 2011, He and Hubbell, 2012, He and Hubbell, 2013), but it is known that species losses will continue to occur due to biotic relaxation (Diamond, 1972, Heywood et al., 1994, Tilman et al., 1994), potentially over a long period of time (Diamond, 1972, Halley et al., 2014). Recent theoretical studies have found both species- and endemics-area based methods underestimate extinction (Rybicki and Hanski, 2013, Matias et al., 2014). Development of species-area based methods continues with examples including extensions of the power-law species-area relationship to incorporate differences in habitat heterogeneity (Triantis et al., 2003), degree of landscape fragmentation (Hanski et al., 2013), and how species perceive and use the habitat matrix

(Pereira and Daily, 2006, Koh and Ghazoul, 2010, Koh et al., 2010). I provide a new application and extension of the endemics-area method, allowing patch-scale losses to be probabilistically accumulated to estimate regional extinctions, adding to the available tools for predicting extinction. There is potential to extend the approach to incorporate biological interactions, for example, adjusting sampling probabilities according to changes in dispersal, which could affect long-term *equilibrium* carrying capacity of the new landscape geometry—the subject of ongoing theoretical investigation (Mouquet et al., 2011, Rybicki and Hanski, 2013, Halley et al., 2014, Matias et al., 2014).

I found the complete removal of small wetlands resulted in the highest risk to regional species diversity for a given decrease in the total area of the regional wetland estate. Neither area nor total richness was correlated with the number of endemic species and some small wetlands contained many endemics. This somewhat counterintuitive finding suggests susceptibility of wetland vegetation to regional species loss even when only a few, small wetlands are destroyed. Incorporating both area- and patch-loss scenarios in similar work is important because of the possible differences in extinction estimates that can arise. My modelling approach is readily transferrable to other systems with island-like ecosystems dispersed across a hostile matrix, including forest fragments and coral reefs.

References

ALAHUHTA, J., HEINO, J. & LUOTO, M. 2011. Climate change and the future distributions of aquatic macrophytes across boreal catchments. *Journal of Biogeography,* 38**,** 383-393.

BALIAN, E. V., SEGERS, H., LEVEQUE, C. & MARTENS, K. 2008. The freshwater animal diversity assessment: An overview of the results. *Hydrobiologia,* 595**,** 627-637.

BROCK, M. A. & CASANOVA, M. T. 1997. Plant life at the edges of wetlands: ecological responses to wetting and drying patterns. *In:* KLOMP, N., LUNT, I. (ed.) *Frontiers in Ecology: Building the Links.* Oxford: Elsevier.

BROOK, B. W., SODHI, N. S. & NG, P. K. L. 2003. Catastrophic extinctions follow deforestation in Singapore. *Nature,* 424**,** 420-423.

BROOKS, T. M., PIMM, S. L. & COLLAR, N. J. 1997. Deforestation predicts the number of threatened birds in insular southeast Asia. *Conservation Biology,* 11**,** 382-394.

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.

CASANOVA, M. T. 2011. Using water plant functional groups to investigate environmental water requirements. *Freshwater Biology,* 56**,** 2637-2652.

CHARLES, S. P. & FU, G. 2014. *Statistically Downscaled Projections for South Australia - Task 3 CSIRO Final Report,* Adelaide, South Australia, Goyder Institute for Water Research, Technical Report Series No. 15/1.

CONNOR, E. F. & MCCOY, E. D. 1979. Statistics and biology of the species-area relationship. *American Naturalist,* 113**,** 791-833.

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DAHL, T. E. 2011. Status and trends of wetlands in the conterminous United States 2004 to 2009 *In:* SERVICE, F. A. W. (ed.). Washington, D.C.: U.S. Department of the Interior.

DAVIDSON, N. C. 2014. How much wetland has the world lost? Long-term and recent trends in global wetland area. *Marine and Freshwater Research,* 65**,** 934-941.

DAVIES, B., BIGGS, J., WILLIAMS, P., WHITFIELD, M., NICOLET, P., SEAR, D., BRAY, S. & MAUND, S. 2008. Comparative biodiversity of aquatic habitats in the European agricultural landscape. *Agriculture Ecosystems & Environment,* 125**,** 1-8.

DELLA BELLA, V., BAZZANTI, M., DOWGIALLO, M. G. & IBERITE, M. 2008. Macrophyte diversity and physico-chemical characteristics of Tyrrhenian coast ponds in central Italy: implications for conservation. *Hydrobiologia,* 597**,** 85-95.

DIAMOND, J. M. 1972. Biogeographic kinetics - estimation of relaxation-times for avifaunas of southwest Pacific islands. *Proceedings of the National Academy of Sciences of the United States of America,* 69**,** 3199-&.

DUDGEON, D., ARTHINGTON, A. H., GESSNER, M. O., KAWABATA, Z. I., KNOWLER, D. J., LEVEQUE, C., NAIMAN, R. J., PRIEUR-RICHARD, A. H., SOTO, D., STIASSNY, M. L. J. & SULLIVAN, C. A. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews,* 81**,** 163-182.

EHRLICH, P. R. & EHRLICH, A. H. 1981. *Extinction: The Causes and Consequences of the Disappearance of Species,* New York, Random House.

ESSL, F., DULLINGER, S., MOSER, D., RABITSCH, W. & KLEINBAUER, I. 2012. Vulnerability of mires under climate change: implications for nature conservation and climate change adaptation. *Biodiversity and Conservation,* 21**,** 655-669.

FLINN, K. M., LECHOWICZ, M. J. & WATERWAY, M. J. 2008. Plant species diversity and composition of wetlands within an upland forest. *American Journal of Botany,* 95**,** 1216-1224.

GIAM, X., TING HUI, N., LOK, A. F. S. L. & HEOK HEE, N. 2011. Local geographic range predicts freshwater fish extinctions in Singapore. Journal of Applied Ecology, 48, 356-363

GIAM, X. L., KOH, L. P., TAN, H. H., MIETTINEN, J., TAN, H. T. W. & NG, P. K. L. 2012. Global extinctions of freshwater fishes follow peatland conversion in Sundaland. *Frontiers in Ecology and the Environment,* 10**,** 465-470.

GIBSON, L., LYNAM, A. J., BRADSHAW, C. J. A., HE, F., BICKFORD, D. P., WOODRUFF, D. S., BUMRUNGSRI, S. & LAURANCE, W. F. 2013. Near-Complete Extinction of Native Small Mammal Fauna 25 Years After Forest Fragmentation. *Science,* 341**,** 1508-1510.

GRACE, J. B. & WETZEL, R. G. 1981. Habitat partitioning and competitive displacement in cattails (Typha) - experimental field studies. *American Naturalist,* 118**,** 463-474.

HALLEY, J. M., SGARDELI, V. & MONOKROUSOS, N. 2013. Species-area relationships and extinction forecasts. *Year in Ecology and Conservation Biology,* 1286**,** 50-61.

HALLEY, J. M., SGARDELI, V. & TRIANTIS, K. A. 2014. Extinction debt and the species-area relationship: a neutral perspective. *Global Ecology and Biogeography,* 23**,** 113-123.

HANSEN, M. C., STEHMAN, S. V., POTAPOV, P. V., LOVELAND, T. R., TOWNSHEND, J. R. G., DEFRIES, R. S., PITTMAN, K. W., ARUNARWATI, B., STOLLE, F., STEININGER, M. K., CARROLL, M. & DIMICELI, C. 2008. Humid tropical forest clearing from 2000 to 2005 quantified by using multitemporal and

multiresolution remotely sensed data. *Proceedings of the National Academy of Sciences of the United States of America,* 105**,** 9439-9444.

HANSKI, I., ZURITA, G. A., ISABEL BELLOCQ, M. & RYBICKI, J. 2013. Species-fragmented area relationship. *Proceedings of the National Academy of Sciences of the United States of America,* 110**,** 12715-12720.

HARTE, J. & KINZIG, A. P. 1997. On the implications of species-area relationships for endemism, spatial turnover, and food web patterns. *Oikos,* 80**,** 417-427.

HAUKOS, D. A. & SMITH, L. M. 1994. The importance of playa wetlands to biodiversity of the Southern High Plains. *Landscape and Urban Planning,* 28**,** 83-98.

HE, F. & HUBBELL, S. P. 2011. Species-area relationships always overestimate extinction rates from habitat loss. *Nature,* 473**,** 368-71.

HE, F. & HUBBELL, S. P. 2012. Extinction and climate change He and Hubbell reply. *Nature,* 482**,** E5-E6.

HE, F. L. & HUBBELL, S. 2013. Estimating extinction from species-area relationships: why the numbers do not add up. *Ecology,* 94**,** 1905-1912.

HEYWOOD, V. H., MACE, G. M., MAY, R. M. & STUART, S. N. 1994. Uncertainties in extinction rates. *Nature,* 368**,** 105-105.

HOLLAND, C. C., HONEA, J. E., GWIN, S. E. & KENTULA, M. E. 1995. Wetland degradation and loss in the rapidly urbanizing area of Portland, Oregon. *Wetlands,* 15**,** 336-345.

HONNAY, O., HERMY, M. & COPPIN, P. 1999. Effects of area, age and diversity of forest patches in Belgium on plant species richness, and implications for conservation and reforestation. *Biological Conservation,* 87**,** 73-84.

IBANEZ, I., CLARK, J. S., DIETZE, M. C., FEELEY, K., HERSH, M., LADEAU, S., MCBRIDE, A., WELCH, N. E. & WOLOSIN, M. S. 2006. Predicting biodiversity

change: Outside the climate envelope, beyond the species-area curve. *Ecology,* 87**,** 1896-1906.

JOHNSON, L. A., HAUKOS, D. A., SMITH, L. M. & MCMURRY, S. T. 2012. Physical loss and modification of Southern Great Plains playas. *Journal of Environmental Management,* 112**,** 275-283.

JOHNSTON, C. A. 2013. Wetland Losses Due to Row Crop Expansion in the Dakota Prairie Pothole Region. *Wetlands,* 33**,** 175-182.

KAESER, M. J. & KIRKMAN, L. K. 2009. Estimating total plant species richness in depressional wetlands in the Longleaf Pine ecosystem. *Wetlands,* 29**,** 866-874.

KINZIG, A. P. & HARTE, J. 2000. Implications of endemics-area relationships for estimates of species extinctions. *Ecology,* 81**,** 3305-3311.

KOH, L. P. & GHAZOUL, J. 2010. A matrix-calibrated species-area model for predicting biodiversity losses due to land-use change. *Conserv Biol,* 24**,** 994-1001.

KOH, L. P., LEE, T. M., SODHI, N. S. & GHAZOUL, J. 2010. An overhaul of the species-area approach for predicting biodiversity loss: incorporating matrix and edge effects. *Journal of Applied Ecology,* 47**,** 1063-1070.

MALCOLM, J. R., LIU, C. R., NEILSON, R. P., HANSEN, L. & HANNAH, L. 2006. Global warming and extinctions of endemic species from biodiversity hotspots. *Conservation Biology,* 20**,** 538-548.

MALTCHIK, L., ROLON, A. S. & STENERT, C. 2010. Aquatic macrophyte and macroinvertebrate diversity and conservation in wetlands of the Sinos River basin. *Brazilian Journal of Biology,* 70**,** 1179-1184.

MATIAS, M. G., GRAVEL, D., GUILHAUMON, F., DESJARDINS-PROULX, P., LOREAU, M., MUENKEMUELLER, T. & MOUQUET, N. 2014. Estimates of

species extinctions from species-area relationships strongly depend on ecological context. *Ecography,* 37**,** 431-442.

MAY, R. M., LAWTON, J. H. & STORK, N. E. 1995. *Assessing extinction rates*.

MOUQUET, N., MATTHIESSEN, B., MILLER, T. & GONZALEZ, A. 2011. Extinction Debt in Source-Sink Metacommunities. *Plos One,* 6.

PEINTINGER, M., BERGAMINI, A. & SCHMID, B. 2003. Species-area relationships and nestedness of four taxonomic groups in fragmented wetlands. *Basic and Applied Ecology,* 4**,** 385-394.

PEREIRA, H. M., BORDA-DE-AGUA, L. & MARTINS, I. S. 2012. Geometry and scale in species-area relationships. *Nature,* 482**,** E3-4; author reply E5-6.

PEREIRA, H. M. & DAILY, G. C. 2006. Modeling biodiversity dynamics in countryside landscapes. *Ecology,* 87**,** 1877-1885.

PIMM, S. L. & ASKINS, R. A. 1995. Forest losses predict bird extinctions in eastern North America. *Proceedings of the National Academy of Sciences of the United States of America,* 92**,** 9343-9347.

POIANI, K. A. & JOHNSON, W. C. 1993. Potential effects of climate-change on a semi-permanent prairie wetland. *Climatic Change,* 24**,** 213-232.

PRENDERGAST, J. R., QUINN, R. M., LAWTON, J. H., EVERSHAM, B. C. & GIBBONS, D. W. 1993. Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature,* 365**,** 335-337.

R CORE TEAM 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

RODRIGUES, A. S. L. & GASTON, K. J. 2001. How large do reserve networks need to be? *Ecology Letters,* 4**,** 602-609.

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ROSSET, V., LEHMANN, A. & OERTLI, B. 2010. Warmer and richer? Predicting the impact of climate warming on species richness in small temperate waterbodies. *Global Change Biology,* 16**,** 2376-2387.

RYBICKI, J. & HANSKI, I. 2013. Species-area relationships and extinctions caused by habitat loss and fragmentation. *Ecology Letters,* 16**,** 27-38.

SCHEFFER, M., VAN GEEST, G. J., ZIMMER, K., JEPPESEN, E., SONDERGAARD, M., BUTLER, M. G., HANSON, M. A., DECLERCK, S. & DE MEESTER, L. 2006. Small habitat size and isolation can promote species richness: second-order effects on biodiversity in shallow lakes and ponds. *Oikos,* 112**,** 227-231.

SIMBERLOFF, D. & GOTELLI, N. 1984. Effects of insularization on plant-species richness in the prairie-forest ecotone. *Biological Conservation,* 29**,** 27-46.

SMITH, A. B. 2010. Caution with curves: Caveats for using the species-area relationship in conservation. *Biological Conservation,* 143**,** 555-564.

SODHI, N., BROOK, B. & BRADSHAW, C. 2009. Causes and consequences of species extinctions. *In:* LEVIN, S. E., CARPENTER, S., GODFRAY, H., KINZIG, A., LOREAU, M., LOSOS, J., WALKER, B., DS, W. & EDS.), A. (eds.) *The Princeton Guide to Ecology.* Princeton, New Jersey, USA: Princeton University Press.

STEVENS, A. 2006. Fleurieu Peninsula Swamp Vegetation Survey 2006 Floristic Definition of the Fleurieu Peninsula Swamps. Adelaide.

STRÖM, L., JANSSON, R. & NILSSON, C. 2012. Projected changes in plant species richness and extent of riparian vegetation belts as a result of climate-driven hydrological change along the Vindel River in Sweden. *Freshwater Biology,* 57**,** 49-60.

TILMAN, D., MAY, R. M., LEHMAN, C. L. & NOWAK, M. A. 1994. Habitat destruction and extinction debt. *Nature,* 371**,** 65-66.

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TRIANTIS, K. A., MYLONAS, M., LIKA, K. & VARDINOYANNIS, K. 2003. A model for the species-area-habitat relationship. *Journal of Biogeography,* 30**,** 19-27.

ULRICH, W. 2005. Predicting species numbers using species-area and endemics-area relations. *Biodiversity and Conservation,* 14**,** 3351-3362.

XENOPOULOS, M. A. & LODGE, D. M. 2006. Going with the flow: Using species-discharge relationships to forecast losses in fish biodiversity. *Ecology,* 87**,** 1907-1914.

ZURLINI, G., GROSSI, L. & ROSSI, O. 2002. Spatial-accumulation pattern and extinction rates of Mediterranean flora as related to species confinement to habitats in preserves and larger areas. *Conservation Biology,* 16**,** 948-963.

Chapter 5   Conclusions

My results have improved the understanding of wetland plant biodiversity, how it is distributed across an agricultural landscape, which mechanisms are important in structuring community composition, and where the major extinction risks lie. From a theoretical perspective, I showed how existing area-based models can be modified to predict extinction risk in discrete habitat patches, something never before attempted, but urgently required. The approach I developed has low data and programming requirements relative to other emerging methods, yet is flexible and general enough to be applied in any terrestrial or marine ecosystem occuring in discrete patches.

This body of research produced important ecological and practical insights relating to the distribution of native plant biodiversity between patches of discrete wetland habitat in an agricultural matrix. I showed in Chapter 2 that these wetlands provide important refuges for terrestrial, as well as obligate wetland native plants and thus provide an unrecognised regional contribution to biodiversity conservation for terrestrial plant species. I quantified the surprisingly large contribution that these terrestrial plants make to wetland biodiversity, which exceeds 40 % of regional richness across Fleurieu Peninsula wetlands. By providing a distributed network of patches of native biodiversity, Fleurieu wetlands reduce extinction risk across the landscape that likely extends beyond the plant community.

In Chapter 2 I also showed that neither wetland size nor species richness determine the regional conservation value of an individual Fleurieu wetland. Endemic species are unpredictably distributed, but Chapter 3 suggested that competitive pressures are higher in wetlands that occur in clusters; some isolation appears to be an important determinant of both endemicity and more unique species composition. The results of Chapter 3 also showed that proximity to source populations does not appear to be critical for compositional uniqueness. In fact, a little isolation might be beneficial to Fleurieu wetlands,

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an unusual finding that runs counter to conventional understanding and warrants further investigation. Chapter 3 showed that community assembly processes are complex and interact with one another and suggests that future wetland investigations on this topic should consider how niche, competitive and dispersal based mechanisms interact.

The most important findings are undoubtedly contained in Chapter 4: extinction risk from loss of individual wetlands is much higher than for an equivalent reduction in area, and is highest if small wetlands are removed first. Comparable findings have been suggested in various patch habitats before, but never quantified until now. In hindsight, this finding could perhaps have been predicted, considering what I have shown about the way that endemic species are distributed and how species composition arises. The future challenge for conservation biologists and wetland managers is to determine how general this finding is—small wetlands are almost certainly at greater risk from global change. Given that I am not the first to find a disproportionate representation of endemic species in smaller patches within cleared landscapes, a comparison between similar patch habitat types under natural and modified conditions would be interesting.

From a more technical perspective, a possible extension to the methods I developed would be to use a Bayesian inferential framework for wetland-scale species losses. Sampling probabilistically from the empirical endemics-area relationship rather than using the worst-case 95 % confidence limit to predict wetland-scale losses for a loss in area (i.e., Chapter 4) would arguably provide a more defensible estimate of imminent extinction. From a biological and practical point of view, the method is flexible enough to incorporate different autecological knowledge, or specific spatial relationships, through the way that species prediction risk is assigned. For example, the implementation in Chapter 4 used only the species richness of the wetland before the change in area and the sampling probability assigned at species level to select species for removal. It would be a straightforward matter

to encode more sophisticated rules relating to autecology, e.g., to alter the probability of removing species based on their dispersal potential and the proximity of source populations.

The major problem for this work was obtaining adequate data, and this is also the major weakness. I used a combination of large wetland databases, survey records and some of my own data, originally anticipating having up to an order of magnitude more replicate wetlands (there were vegetation survey data recorded from 219 wetlands). Detailed data checking revealed that most wetlands likely had species lists that were incomplete. In Chapter 4, I supplemented the database with data that I personally collected during my Masters. Had time and resources allowed more extensive data collection, I would have a greater opportunity to explore more sophisticated modelling techniques, including Bayesian applications. It could also have allowed detailed inventory of additional wetlands, providing increased replication.

Additional uncertainty is associated with the use of the generalized endemics-area relationship. It remains unverified how well the use of multiple grids in different vegetation types would generalize to a larger-scale endemics-area curve built on data collected over tens of hectares in a wetland environment. Owing to the physical difficulties of surveying dense, wetland vegetation it seems unlikely such data will ever be available for validation. The general approach could possibly be validated using stem-mapped datasets, such as those collected under the Center for Tropical Forest Science and Forest Global Earth Observatories protocols (http://www.ctfs.si.edu/group/), testing how well small grids predict the pattern of the overall endemics-area relationship.

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