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Dispersal-driven homogenization of wetland vegetation revealed from local contributions to β-diversity

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Abstract

Questions: Within a meta-community, what determines how local species composition differs from the regional community? How do local conditions and landscape context affect this differentiation in wetland vegetation?

Location: Fleurieu Peninsula, South Australia.

Methods: We sampled native vegetation across 26 hydrological gradients in a wetland meta-community within a heavily cleared agricultural landscape. We used the local contribution to β-diversity to quantify how species composition at each site differed from the average across all sites. We hypothesized that local contribution to β-diversity would respond to assembly processes (niche, biological interactions, dispersal) through effects on the species turnover and richness difference components of β-diversity. We used beta regression to model local contribution to β-diversity, building a candidate set of 55 models, each incorporating one of the assembly processes. We used standardized regression coefficients to measure effect size, and null models to explore diversity patterns further.

Results: While variations in among-site niche dimensions were influential, the strongest control on local contribution to β-diversity was a negative association with the number of wetlands within 200 m. Null models showed this was because common species were over-represented in well-connected sites within the meta-community, while rare species were under-represented.

Conclusions: Our results demonstrate the homogenization of native plant species composition in well-connected wetlands, consistent with theoretical predictions of declining β-diversity when connectivity is high. We recommend comparative analysis of local species composition to regional average diversity to evaluate the role of wetland connectivity in homogenization of composition before conservation or restoration priorities are assigned.

Introduction

Variation in species composition among a group of sites – their β-diversity (Whittaker 1960) – can be partitioned to reveal the individual contribution made by each site to the overall total (Legendre & De Caceres 2013). This local contribution to β-diversity quantifies the difference in species composition of each site relative to the average composition across all sites in the landscape (Legendre & De Caceres 2013). Sites that contribute more than the landscape mean local contribution to β-diversity have species compositions that are relatively unusual within the landscape, and therefore have potentially high conservation value (Legendre & De Caceres 2013; Legendre 2014).

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Understanding why some sites have high local contribution to β-diversity could therefore be important for conservation prioritization and management decision-making. For example, regional plant diversity in many wetland systems depends more on differences in species composition among wetlands than on wetland-scale diversity (e.g. Freestone & Inouye 2006; Sasaki et al. 2012; Deane et al. 2016, 2017); local contribution to β-diversity provides a means to identify which sites in a meta-community contribute the most to regional diversity and why. Wetlands are an ideal model system to explore this topic, because they represent definable habitat patches that differ both in their local abiotic conditions and degree of connectivity across the landscape.

Differences in local contribution to β-diversity can arise through species turnover (also called 'species replacement') or richness difference (also called 'nestedness') components of β-diversity, or both (Legendre 2014). The relative importance of these components will in turn reflect how each community assembles from the regional species pool. These community assembly processes can be divided into three primary drivers: (1) niches, (2) biological interactions (e.g. competition) and (3) dispersal (Hubbell 2001; Hille Ris Lambers et al. 2012). Niche-based explanations of species assembly (e.g. Hutchinson 1957) focus on the role of environmental heterogeneity and species-level differences in relative fitness. The spatial scale of heterogeneity in abiotic conditions is hypothesized to determine how richness differences and species turnover affect local contribution to β-diversity. For example, an influential niche dimension for wetlands is the availability of water. Wetlands with the most diverse range of hydrological conditions – from short-term surface saturation to permanent inundation, along with a range of intermediate depth and duration combinations – can sample most widely from the regional species pool. Such sites often have the highest species richness (e.g. Shi et al. 2010), potentially increasing local contribution to β-diversity due to richness differences compared to less heterogeneous sites. However, if hydrology varies little within wetlands, but markedly among them, this hypothesis predicts greater species turnover among sites through habitat filtering (Keddy 1992). Local contribution to β-diversity would then likely depend more on site-level differences in abiotic conditions, with extreme conditions potentially supporting regionally rare species and high local contribution to β-diversity.

Co-existence depends not only on species' niche differences, but also on differences in relative fitness (Chesson 2000), where competitive exclusion can result in the loss of inferior species that are too functionally similar (Hille Ris Lambers et al. 2012). More fertile environments can reduce diversity through this mechanism when: (1) competition constrains species establishment (Huston 1994), (2) fewer species are adapted to such highly productive environments (Taylor et al. 1990) or (3) releasing species from nutrient limitation favours certain species that exclude competitively inferior ones (Suding et al. 2005; Liu et al. 2017). A unimodal species–biomass response has been observed in wetlands where diversity peaks at intermediate biomass, but high-biomass wetlands have fewer species (Keddy 2005). Species abundance distributions universally show that few species occur in high abundance while most are rare (McGill et al. 2007); these abundant species would likely be prominent in high-biomass wetlands. A community dominated by the most abundant species in a region would be close to the regional average composition and of low local contribution to β-diversity.

In entirely dispersal-driven assembly species composition represents a balance between colonization and extinction (MacArthur & Wilson 1967; Hubbell 2001). Isolated wetlands tend to have fewer species than expected for their size (e.g. Boughton et al. 2010), where only the strongest dispersers can reach the most isolated wetlands. In this case, the effect of dispersal on local contribution to β-diversity is likely to be a trade-off between reduced diversity in more isolated sites, but more rapid species turnover of rare species across the landscape (Economo & Keitt 2008; Minor et al. 2009).

Recent studies examining community assembly processes in wetlands have been equivocal, concluding that biological interactions (Chmara et al. 2013), dispersal (Boughton et al. 2010) or niche-related processes (Flinn et al. 2010; Douda et al. 2012) dominate. Our explicit aim was not to determine whether one process dominates assembly, but how the effect of these processes on the local composition of wetland plant communities determines their variation from the regional, average species composition. Using plant survey data from a network of seasonal wetlands in temperate South Australia, we tested how local conditions and landscape setting affect the extent to which the resulting species composition varies from the regional average (i.e. local contribution to β-diversity). We hypothesized that local contribution to β-diversity would: (1) increase due to local or regional heterogeneity if niche-based processes dominated, through richness differences and turnover, respectively; (2) decrease monotonically with biomass due to competitive exclusion of non-dominant species; and (3) increase in wetlands where dispersal was limited.

Methods

Study region and wetland character

The study region was the Fleurieu Peninsula, South Australia (Fig. 1), centred on latitude 35.5°S. The region's climate is mediterranean, with warm, dry summers and cool,

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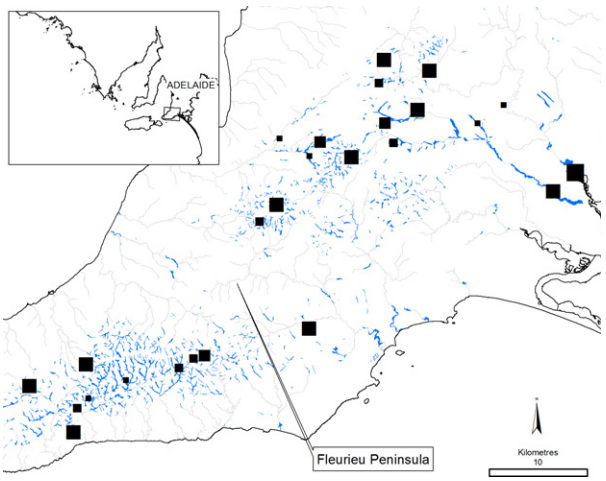

Fig. 1. Study region in South Australia showing all wetlands, with study wetlands represented by symbols proportional to their local contribution to beta diversity. Larger symbols represent wetlands with more unique species compositions. [Colour figure can be viewed at wileyonlinelibrary.com]

wet winters (mean annual rainfall <900 mm). Over 850 wetlands have been mapped on the Fleurieu Peninsula, mostly associated with low-order (Appendix S1) intermittent streams in higher rainfall upland areas of the central peninsula (Fig. 1; Deane et al. 2016). The region has been heavily cleared of native vegetation and wetlands of all sizes represent important reservoirs of native plant diversity in the mixed agricultural matrix (Deane et al. 2017).

Wetlands range from waterlogged to seasonally inundated, but maximum depths are typically <20 cm. Dense heathy or reedy vegetation communities comprise up to three distinct strata in a structural mosaic (Deane et al. 2012). The upper stratum comprises a medium-tall shrub layer dominated by tea tree (*Leptospermum* spp.), the intermediate stratum is generally a tall mixed sedge (Restionacaeae or Cyperaceae) or sedge–fern association (particularly the ferns *Blechnum minus* and *Gleichenia microphylla*), while the groundcover layer comprises mixed herbs, grasses or low-lying sedges (Deane et al. 2012).

Data

Field data were collected during autumn 2006. We selected 26 wetlands with a consistent sampling effort, each surveyed using five quadrats. At each wetland, a transect was established along the major hydrological gradient and vegetation was sampled in non-nested 5 × 2 m quadrats, with the longer axis oriented along contours of the hydrological gradient to minimize variation in the hydrological conditions for each. Taxonomic resolution was to species, and the cover of each species was recorded in the field using a modified Braun-Blanquet scoring system (Braun-Blanquet 1932). Quadrats were spaced at intervals 20–50 m apart, with actual spacing selected subjectively to sample variation in broad structure and composition, while avoiding wetland edges. Prior to analysis, we confirmed this variable spacing did not affect within-site β-diversity (Appendix S2). The sampling design (i.e. five samples spaced along a water availability gradient) allows inference on species composition and density (number of species per 50 m^2; Gotelli & Colwell 2001) across the hydrological coenocline at each site. We converted cover scores to percentage cover representing mid-points of each cover class and averaged these for all quadrats to obtain a single, site-level vegetation sample.

Biomass was quantified independently of the taxonomic data using a touch pole method. The number of touches within a conceptual 5-cm diameter cylinder discretized to 0.2 m vertical 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, other field data collected were: soil moisture (seven-level ordinal scale 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. We calculated the mean and coefficient of variation for each variable over the five quadrats to create site-level measures of environmental patterns and their variability. As we were interested in the competitive effect of exotic species on composition, we used total exotic plant cover as a predictor, removing exotic species before calculating community composition (see Appendix S3 for results including exotic species). We retained native terrestrial species because they are an important component of wetland plant diversity in the region (Deane et al. 2016, 2017). All data used in modelling are provided in Appendix S4.

Response and predictor variables

We used pair-wise Bray-Curtis (Bray & Curtis 1957) dissimilarities calculated between all pairs of the 26 wetlands as a measure of total β-diversity (Mellin et al. 2014). As a response variable, we used the 'local contribution to β-diversity' metric (Legendre & De Caceres 2013; 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 site to the centroid of the distribution (the site-level sum of squares) and the total sum of squares for the pair-wise dissimilarity matrix (Legendre & De Caceres 2013).

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We used mapped boundaries from a State wetland inventory project (Harding 2005) to define the extent of individual wetlands. In addition to the field-measured variables, we calculated or derived 21 environmental predictors (Appendix S2, S4) using spatial data on wetland shape, soil type, topography, hydrology, roads, land use and native vegetation cover within a 200-m buffer around each wetland. Our choice of a 200-m buffer distance was subjective, but based on the ability to discriminate between wetlands; larger buffers (e.g. 500–1000 m) resulted in similar values for predictors owing to the density of wetlands in the region (mean ± SD distance to the ten nearest wetlands = 1494 ± 944 m; Fig. 1). We centred and re-scaled all input variables by two SD i.e. $x' = (x - \bar{x}/\ 2\sigma_x^2)$ to allow direct comparison of effect sizes in model-averaged coefficients among binary and continuous predictors (Gelman 2008). We tested all variables for collinearity, removing any with a Pearson's $|r| > 0.6$, where we omitted variables with the least plausible biological relationship with one of the hypothesized mechanisms (see Introduction).

Modelling overview

We used an information theoretic framework, dividing the analysis into two stages to reduce the number of variables used to infer the most important mechanisms of community assembly: (1) first, we compared support for the individual effects for each hypothesized mechanism separately (Stage I; i.e. niche, biological interactions and dispersal), and (2) then we combined the predictors from the top-ranked models from Stage I to determine their combined effects and relative effect sizes (Bradshaw et al. 2014).

Model structures

For the Stage I analysis, we built three model subsets, each using only variables that were proxy measures for one of the three hypotheses (Bradshaw et al. 2014). That is, we did not combine niche-based predictors with those measuring dispersal or competition into a single model. We built models using linear, quadratic and interaction terms where unimodal (hump-shaped) or multiplicative relationships were biologically plausible for the variables concerned (model structures and their rationale are described in Appendix S5). To avoid over-fitting, we used three or fewer predictors in any one model to maintain a ratio of data to predictors close to 10.

Model fitting

Local contributions to beta diversity take values from 0 to 1, so we used β regression (Ferrari & Cribari-Neto 2004) to fit the candidate set of models. β regression, based on the two-parameter β distribution, was proposed by Ferrari & 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 GLM, with the response variable modelled via a link function (usually the logit) and a linear predictor, with the model optimized via maximum likelihood (Ferrari & Cribari-Neto 2004). We constructed all β regression models using the R package betareg (Cribari-Neto & Zeileis 2010).

Model comparison and inference

We compared and ranked all models using Akaike's information criterion corrected for small sample size (AIC_c; Burnham & Anderson 2002; Grueber et al. 2011). The aim of the Stage I analysis was to identify those predictors that individually explained the most variation in local contributions to β-diversity. In Stage I we therefore selected a conservative, interim final model set using evidence ratios, selecting models where the ratio of the AIC_c weights for the top-ranked models <8, which equates to a difference of at least ~4 in AIC_c units (Burnham & Anderson 2002; Grueber et al. 2011). Having identified the models with the most support in Stage I, we used the predictors from those models in Stage II to build a final global model. We included only additive combinations of variables in the global model (i.e. no interactions) to retain adequate degrees of freedom. We used all subsets selection (Burnham & Anderson 2002) to build a candidate set of models and calculated model-averaged coefficients for all variables from the 95% confidence set based on $wAIC_c$. For any predictor not present in a model, we set the coefficient to zero for model averaging (Grueber et al. 2011). We calculated SE and parameter estimates based on the unconditional variance, which accounts for model selection uncertainty (Burnham & Anderson 2002) and report these as a measure of effect size for each variable. We inferred support for the different hypotheses based on both the identities of predictors in the 95% confidence model set and their averaged coefficient values.

Tests for confounding influences

In addition to the three main hypotheses, we also considered two possible confounding mechanisms: (1) passive sampling, where larger wetlands attract more rare species and therefore have more unique compositions simply because they represent a larger target (Connor & McCoy 1979), and (2) spatial autocorrelation, where nearby sites are more similar because of their proximity (Brown 1984). We fit models for area, wetland size and shape including these in the candidate set to test for passive sampling

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effects. To test for spatial dependency in vegetation composition, we used a Mantel test of Euclidean distances in *x*, *y* grid coordinates (UTM Easting and Northing) and the local contributions to β-diversity.

We also tested for non-linear spatial relationships using principal coordinates of neighbour matrices (PCNM; Borcard & Legendre 2002), calculated with R package vegan. However, we found strong linear correlations with at least one environmental predictor for all of these variables ($|r| > 0.6$) and so we did not include any purely spatial variables in the candidate set. Rather, we used variation partitioning (Borcard et al. 1992) in a complementary analysis to quantify directly the importance of spatial structure in the data (Appendix S6).

Post-hoc tests

The results of Stage I and II modelling both suggested local-scale dispersal between wetlands dominated local contribution to β-diversity (see Results). To elaborate this finding, we did a *post-hoc* analysis of pair-wise β-diversity, partitioning it into turnover and richness difference components and testing the importance of the environmental predictors independently following Legendre (2014). Results of this *post-hoc* analysis are presented in Appendix S7, with more detailed analysis of species composition patterns in Appendix S8.

We further hypothesized that if short-range dispersal increased the probability that competitively superior species would reach a wetland, this could exclude other species from establishing with a disproportionate impact on rare species (Huston 1994; Keddy 2005). We therefore used a null model approach to test for any effects of dispersal probability on the distribution of common and rare species. We first classified wetlands into dispersal groups based on the number of wetlands found within 200 m (0, 1, 2 and ≥3 wetlands, maximum 6), which gave a similar number of wetlands in each group (7, 7, 6 and 6, respectively). We then calculated the proportion of total observed wetland richness that comprised common species (found at ≥8 wetlands – the 75th occupancy percentile) and rare species (found at ≤2 wetlands) as a function of the dispersal groups. We compared the distribution of the observed proportion of common and rare species in each dispersal group with the predictions of a null model. For the null model, rather than using the observed species data, we simulated null communities of the same species richness as the observed data by resampling without replacement. Here each species' sampling probability in the simulated wetland data set was based on their occupancy across all wetlands (Abele & Patton 1976; Connor & Simberloff 1978). We then again calculated the proportion of common and rare species in each wetland in each dispersal group and compared their distributions.

The sample size in our main data set was small ($n = 26$), so we repeated these null model simulations using an independent data set that includes 75 wetlands from the same region (Deane 2016). These additional data represent wetland-scale diversity, so they also can be used to test the relationship at this broader scale (Appendix S9). Note that these data comprise only species lists and were not therefore suitable for the main analysis.

We did all modelling and analysis in the R language (R Foundation for Statistical Computing, Vienna, AT, US) using the custom R function 'LCBD.comp' provided in Legendre (2014) to calculate the local contributions to β-diversity, and packages arm, betareg, vegan and MuMIn for model comparison and averaging as described above (Cribari-Neto & Zeileis 2010). We tested for the generalized variance inflation factor of predictors in the global model using package car (Fox & Weisberg 2011).

Results

Total observed richness was 113 native and 17 exotic vascular plant species. Native species density for quadrats and sites was (mean [± 95% confidence limits]) 8.7 [8.03, 9.34] and 21 [17.8, 23.3], respectively. Local contributions to β-diversity (range 0.029–0.055; Fig. 1) were not strongly correlated with native species richness (Pearson's $r = -0.23$, $t = -1.14$, $P = 0.26$), nor spatial proximity of wetland centroids (Mantel test $r = 0.06$, $P = 0.13$) and had no relationship with wetland area (Pearson's $r = 0.013$, $t = -0.06$, $P = 0.94$). Pair-wise β-diversity analysis showed species replacement and richness differences accounted for 57% and 43% of total β-diversity among sites, respectively (Appendix S7). Dominant environmental predictors for pair-wise β-diversity for the species replacement component were Soil pH (12.2% of explained variation; Appendix S7) and Wetland count and Peat (22% and 20% of explained variation, respectively; Appendix S7) for richness differences.

Relative support for individual assembly mechanisms

Selecting all 'Stage I' models within 4 ΔAIC_c of the top-ranked model yielded a final set of seven models (Appendix S5), with a cumulative $wAIC_c = 0.73$ (Table 2). Three models in the final set were based on dispersal (including the top-ranked model; Table 2) and two each were based on niche and competitive hypotheses (Tables 1 and 2). These models included eight predictors (Tables 1 and 2, Appendix S5), three each from the niche (Peat, Soil pH, Soil type G) and dispersal (Wetland count, Wetland%, Mean dist5), and two biological predictors (Biomass, Exotic

Table 1. Abbreviation and description of explanatory variables for predictors in the final model set for Stage I (Table 2).

Mechanism	Abbrev.	Description and Rationale
Niche	pH	Mean soil hydrogen ion concentration from all wetland quadrats (range in unstandardized pH units 5.1–8.5).
Niche	Peat	% of wetland samples with peat substrate. Indicator of permanent saturation (range 0–100)
Niche	Soil type G	Percentage of wetland buffer zone area containing soils classified as soil group G (see Appendix S2 for a description)
Dispersal	Wetland%	Percentage of wetland buffer zone area occupied by wetlands other than the site under analysis (range 0–30)
Dispersal	Wetland count	Number of other wetlands within 200 m buffer (range 0–6). Treated as a continuous variable in analysis
Dispersal	Mean dist5	Mean centroid–centroid distance to the nearest five wetlands
Biological	Exotic cover	Mean% cover of exotic species present in the quadrat (range 0–23)
Biological	Biomass	Average of the total number of touch pole hits for the quadrats in each wetland (range 20–136)

A full list of variables and explanation of their calculation appears in Appendix S1.

Table 2. Stage I final model set and model ranking values for individual comparisons of hypotheses. Predictors are described in Table 1 and their standardized regression coefficients are shown in Fig. 2; *df* is the model degrees of freedom; AIC_c is Akaike's information criterion corrected for small sample size; $wAIC_c$ is the small sample-corrected AIC_c weight; ΔAIC is the difference in Akaike's information criterion compared with the minimum AIC_c; *ER* = evidence ratio, the ratio of the $wAIC_c$ of each model and the top-ranked model. %dev is the percentage of total deviance explained. Model codes indicate the hypothesis on which they are based (dsp = dispersal, bio = biological interactions; phy = physiographic [niche-based]) and a unique identifier (see Appendix S5).

Code	Structure	*df*	AIC_c	$wAIC_c$	ΔAIC_c	*ER*	% dev
dsp03	~Wetland count	3	−183.9	0.25	0	–	31
bio03	~Biomass + exotic cover	4	−182.3	0.11	1.67	2.31	34
bio01	~Biomass	3	−182.2	0.10	1.77	2.43	26
dsp04	~Wetland count + mean dist5	4	−181.9	0.09	2.05	2.79	33
phy02	~pH + soil type G + peat	5	−181.6	0.08	2.29	3.14	39
phy06	~pH	3	−180.6	0.05	3.36	5.36	20
dsp02	~Wetland%	3	−180.5	0.05	3.40	5.48	21

cover). The first model that did not contain at least one of these predictors was ranked 24th in model comparisons ($wAIC_c$ = 0.003; Table S4), suggesting all important predictors were captured in Stage I. The final set of 'Stage I' models explained between 20% and 40% of structural deviance (Table 2).

Relative support for combined assembly mechanisms

A global 'Stage II' model built using the eight predictors from the final model set for individual mechanisms explained 63.5% of total deviance. Despite some correlation among predictors close to our 0.6 threshold for exclusion (Appendix S10), generalized variance inflation factors in the global model were all <2.2 (Appendix S10). None of the predictors in the global model were correlated with species density (Pearson's *r* range [−0.27–0.12], *P* range [0.17-0.98]; Appendix S5). The 95% confidence set of models based on all subsets selection comprised 104 models (Appendix S10). The five top-ranked models included different linear combinations of only four predictors and explained between 47% and 57% of deviance (Table 3). Only the predictor Wetland count (the number of wetlands within 200 m) was consistently included in the five top-ranked models (Table 3; in fact, this appeared in the top 36 ranked models; see Appendix S10). Wetland

Table 3. Stage II model ranking table for the five top-ranked models according to Akaike's information criterion corrected for small sample size (AIC_c). Model structures represent the combined effects of predictors on uniqueness in species composition (quantified as the local contribution to β-diversity).

Model Structure	*k*	LL	AIC_c	$wAIC_c$	ΔAIC_c	% dev
Wetland Count + Peat + Soil pH	5	101.87	−190.74	0.11	–	57
Wetland Count + Peat + Biomass	5	101.49	−189.98	0.07	0.76	57
Wetland Count + Peat	4	99.77	−189.63	0.06	1.11	50
Wetland Count + Soil pH	4	99.33	−188.75	0.04	1.99	47
Wetland Count + Biomass	4	99.30	−188.7	0.04	2.04	49

K, number of model parameters; LL, maximum log-likelihood; AIC_c, Akaike's information criterion corrected for small sample size; $wAIC_c$, small sample-corrected AIC_c weight; ΔAIC, difference in Akaike's information criterion corrected for small sample size compared with the minimum AIC_c; % dev, the percentage of total deviance explained.

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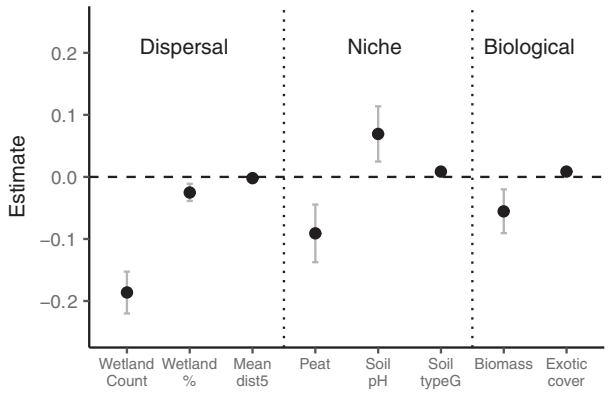

Fig. 2. Standardized regression coefficients for predictor variables in the averaged model. Dotted vertical lines divide the predictors among the respective hypotheses. Averaged regression coefficients (Estimate) were calculated using the zero method (Burnham & Anderson 2002) on the 95% confidence set for the combined effects and indicate relative effect size for the predictor. Error bars show two standard errors calculated from unconditional variance (i.e. including model-selection uncertainty). See Appendix S7 for estimated values.

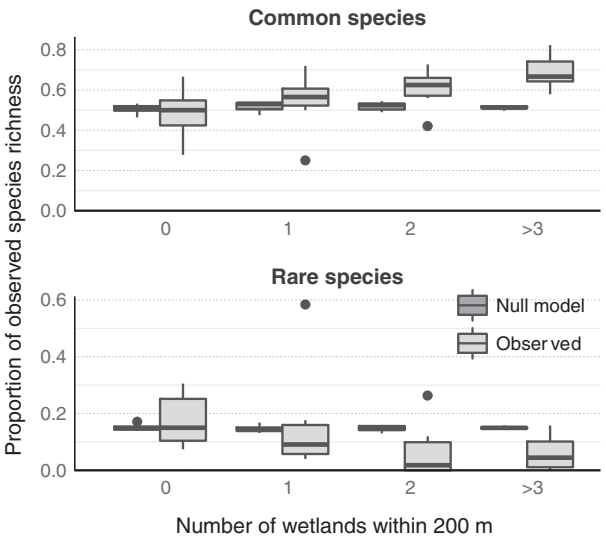

Fig. 3. Comparison of observed proportions of common and rare species with null-model simulations. The proportion of total wetland species richness comprising common (present in ≥ 8 wetlands, n = 24, top panel) and rare (present in ≤ 2 wetlands, n = 54, lower panel) are shown as a function of the number of wetlands within 200 m. Boxplots show the distribution of proportions in each wetland group, with the thick black line indicating the median value for each distribution. The null-model estimate was based on the same species and total occupancies, but these were distributed randomly among wetlands according to observed wetland species richness in each group. The number of wetlands in each connectivity group (*x*-axis categories) were '0' and '1' = 7, '2' and '>3' = 6. The maximum number of wetlands within 200 m in group '>3' was 6.

count had the strongest effect size according to model-averaged regression coefficients, decreasing local contribution to β-diversity as the number of wetlands increased ($\hat{b}_{wc}$ [mean ± SE] = −0.186 ± 0.017; Fig. 2, Appendix S10).

Wetland count also affected the distribution of common and rare species; the proportion of common species increased with this predictor and was higher than expected under a null model (Fig. 3). Conversely, the proportion of rare species decreased with Wetland count (Fig. 3). A virtually identical distribution pattern of common and rare species proportions was evident at wetland scale using an independent data set including 75 wetlands (Appendix S9). Mean species density for the highest and lowest Wetland count groups did not differ (mean [± 95% confidence limits], Group 0 = 23.3 [17.6, 29.0]; Group >3 = 21.2; [18.8, 23.5]), but the variance was higher for more isolated wetlands (Group 0 variance = 55.9; Group >3 variance = 8.2; Bartlett's K^2 = 3.86, df = 1, P = 0.050). Three of seven species indicative of sites from the Group >3 wetlands were sedges or ferns that form dense colonies individually or in association in Fleurieu wetlands (Appendix S8).

The predictors Biomass (representing intensity of biological interactions) and Peat (representing the extent of permanently inundated conditions) both had negative effects on local contributions to β-diversity, although with smaller effect sizes than Wetland count ($\hat{b}_{bm}$ = −0.055 ± 0.018, $\hat{b}_{pt}$ = −0.09 ± 0.023, respectively). Predictors that had positive coefficients on local contribution to β-diversity were Soil pH, Exotic cover and the proportion of Soil type G (Appendix S2) found in the wetland buffer area ($\hat{b}_{ph}$ = 0.069 ± 0.022, $\hat{b}_{ex}$ = 0.008 ± 0.002, $\hat{b}_{sg}$ = 0.014 ± 0.045; Fig. 2, Appendix S10). Variation partitioning confirms the relative importance indicated by regression coefficients, with dispersal, niche and biological interactions explaining 0.24, 0.15 and 0.08 of the variation, respectively. The purely spatial component explained 0.05 of total variation (Appendix S6).

Discussion

We found that all three assembly processes influenced local contribution to β-diversity, but dispersal clearly dominated via its effects on the distribution of common species. Well-connected sites comprised mostly common species, reducing their contribution to β-diversity. Niche-based mechanisms also affected local contribution to β-diversity through the replacement of species along environmental (especially soil pH) gradients across the sites; those sites with harsher conditions had similar species composition, containing only suitably adapted species.

As the number and area of near-neighbour wetlands increased, our sites increasingly comprised regionally

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common species, and concomitantly fewer rare species. This pattern, which was also evident at the wetland scale, suggests dispersal-driven homogenization of vegetation composition across the meta-community. This is consistent with theoretical meta-community models when dispersal is high (Mouquet & Loreau 2003; Economo & Keitt 2008). The role of richness differences in creating this pattern was not due to a systematic variation in species density, but changes in variability. Increasing Wetland count decreased the coefficient of variation in species density by >200% between the least and most well-connected sites; well-connected wetlands were all close to the mean species density, while isolated wetlands varied widely above and below this value.

The question of why Wetland count was a more effective predictor of homogenization than the other spatial predictors we used is interesting, and could relate to the complexity of the wetland network. Based on spatially explicit, theoretical meta-community models for a given migration rate, decreasing the mean distance between all network nodes reduced γ- and β-diversity (Economo & Keitt 2008). Therefore, the Wetland count predictor might represent a proxy for local network topological complexity in the wetland meta-community.

We found that niche effects acted on local contribution to β-diversity via species turnover among sites, rather than increased wetland heterogeneity leading to richness differences. For example, the niche-based predictor Soil pH reflected regional abiotic heterogeneity in this gradient (i.e. among sites), rather than local heterogeneity. Increasing pH was associated with more unique species composition because wetlands with approximately 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 was reduced to less than one-third of the total regional number of species in New York lakes (Weiher & Boylen 1994). More acidic soils did not limit species density, but there was less variation in composition among sites because there were fewer species from which the community could assemble. Hence, harsher conditions imposed limits on site-based composition, leading to a filtering effect (Keddy 1992).

Biomass had no relationship with Wetland count and, therefore, its negative effect on the local contribution to beta diversity appears to be at least partially independent of the dispersal-driven homogenization in composition. Consistent with our prediction that competitively superior species would dominate under more productive conditions, there was no relationship between wetland species density and Biomass, so it was not the result of extensive monospecific stands of vegetation (Hocking et al. 1983; Lavergne & Molofsky 2004). Rather, high-biomass wetlands contained a subset of species drawn from the regional species pool that are capable of co-existing in a productive environment (Taylor et al. 1990). This is broadly consistent with the unimodal species–biomass model, although here we did not observe the expected decrease in species richness (Keddy 2005). This could indicate that there is adequate niche space available at these wetlands to stabilize any competitive differences among species despite their high biomass, thereby maintaining overall diversity.

Our findings illustrate the value of using multiple measures of beta diversity due to the different information they provide (Legendre & De Caceres 2013; Legendre 2014). Modelling local contribution to β-diversity identified how local and regional abiotic conditions, biological interactions and dispersal drive more or less unique species composition, while pair-wise beta diversity confirmed the separate roles of species-turnover and richness differences. The small sample size we used to model local contribution to beta diversity warrants caution in inferring these as general patterns, and also in extrapolating findings to the scale of the entire wetland complex where some predictors might change in importance. We also lacked information on some critical predictors, notably nutrient availability, which could also influence species composition. However, the wetland-scale analysis using the larger data set affords some confidence in our main finding: higher connectivity in these wetlands is associated with homogenization of species composition, decreasing regional conservation value.

As with prior studies investigating community assembly in wetlands (e.g. Boughton et al. 2010; Flinn et al. 2010; Douda et al. 2012; Chmara et al. 2013), a range of interacting mechanisms affected local contributions to beta diversity. From a conservation perspective, wetlands that are most well connected often have the highest species richness (e.g. Boughton et al. 2010). However, elevated α-diversity might not be the best indicator of regional biodiversity importance. We recommend analysis of local species composition against regional average diversity as a means to evaluate the role of wetland connectivity before conservation or restoration priorities are assigned.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Introduction to the wetlands of the Fleurieu Peninsula, and a possible management response to homogenization of wetland native plant species composition.

Appendix S2. Description of all environmental predictors used in modelling and sensitivity test of quadrat spacing.

Appendix S3. Model coefficients for the analysis repeated with exotic species included in the response data.

Appendix S4. Species list and values for all environmental predictors at each site (raw data also provided in a separate comma-separated values file).

Appendix S5 Model comparison results for individual mechanisms (Stage I analysis) and correlation tables.

Appendix S6. Variation partitioning analysis quantifying the separate and shared contributions of spatial, niche, dispersal and biological factors to explained variation.

Appendix S7. Pair-wise β-diversity analysis.

Appendix S8. Multivariate community analysis and indicator species analysis for Wetland count groups.

Appendix S9. Wetland-scale patterns using independent data set of 75 wetlands.

Appendix S10. Model comparison results for combined mechanisms (Stage II analysis).

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