Diversity and Distributions A Journal of Conservation Biogeography

Diversity and Distributions, (Diversity Distrib.) (2010) **16**, 20–32

BIODIVERSITY RESEARCH

Using multi-scale species distribution data to infer drivers of biological invasion in riparian wetlands

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ABSTRACT

Aim Biological invasion is a major conservation problem that is of interest to ecological science. Understanding mechanisms of invasion is a high priority, heightened by the management imperative of acting quickly after species introduction. While information about invading species' ecology is often unavailable, species distribution data can be collected near the onset of invasion. By examining distribution patterns of exotic and native plant species at multiple spatial scales, we aim to identify the scale (of those studied) that accounts for most variability in exotic species abundance, and infer likely drivers of invasion.

Location River Murray wetlands, south-eastern Australia.

Methods A nested, crossed survey design was used to determine the extent of variation in wetland plant abundance, grazing intensity and water depth at four spatial scales (reaches, wetland clumps, wetlands, wetland sections), and among three Depth-strata. We examined responses of exotic and native species groups (grouped into terrestrial and amphibious taxa), native weeds and 10 individual species using hierarchical ANOVA.

Results As a group dominated by terrestrial taxa, exotic species cover varied at reach-, wetland- and section-scales. This likely reflects differences in abiotic characteristics and propagule pressure at these scales. Groups based on native species did not vary at any scale examined. Cover of 10 species mostly varied among and within wetlands (patterns unrelated to species' origin or functional group), but species' responses differed, despite individual plants being similar in size. While flora mostly varied among wetlands, exotic cover varied most among reaches (26%), which was attributed to hydrological modification and human activities.

Main conclusions Multi-scale surveys can rapidly identify factors likely to affect species' distributions and can indicate where future research should be directed. By highlighting disproportionate variation in exotic cover among reaches, this study suggests that flow regulation and human-mediated dispersal facilitate exotic plant invasion in River Murray wetlands.

Keywords

Flow regulation, hierarchical survey design, invasive plant species, River Murray, spatial scale, vegetation.

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INTRODUCTION

Biological invasion is a function of propagule pressure, abiotic and biotic characteristics (Catford *et al.*, 2009). Some of the mechanisms affecting invasion outcomes relate to introduction and dispersal (Lockwood *et al.*, 2005), episodic disturbance and resource availability (Hobbs & Huenneke, 1992; Davis *et al.*, 2000), and biotic interactions that include enemy release and biotic resistance from native species (Keane & Crawley, 2002; Levine *et al.*, 2004). Each of these factors likely takes

DOI:10.1111/j.1472-4642.2009.00631.x
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effect at slightly different spatial and temporal scales. Dispersal limitation, for instance, would typically occur at earlier stages of invasion and at larger spatial scales than community interactions like competition (Belyea & Lancaster, 1999; Catford *et al.*, 2009). Because causal factors produce responses at comparable scales, highlighting scales at which biota vary can help identify factors that cause that biological variation and in doing so provide valuable insights for ecology (Wiens, 1989; Palmer *et al.*, 1997; Fraterrigo & Rusak, 2008).

Determining the relative importance of multiple influential factors remains a key challenge in invasion ecology and is often limited by the ability to observe effects of numerous factors simultaneously. By enabling several scales to be investigated simultaneously, hierarchical designs that nest space and time can identify the scale (of those examined) where there is greatest biological variability and the greatest ecological response (Diez & Pulliam, 2007). This approach is particularly useful when there is little ecological knowledge about factors that may limit species' distributions and abundances, as is often the case with biological invasion (see Buckley, 2008). Foxcroft *et al.* (2009) recently demonstrated the utility of a multi-scale approach for understanding plant invasions in Kruger National Park, South Africa. By highlighting scales of greatest variation in the abundance and distribution of exotic and native species, we posit that multi-scale studies have the potential to indicate factors that drive invasion outcomes.

In this study, we use a hierarchical approach to examine patterns in native and exotic vegetation in riparian wetlands of the River Murray, south-eastern Australia across four spatial scales and among three Depth-strata in one time-period. Riparian ecosystems are among the most invaded types of habitats (Hood & Naiman, 2000) and, because many of the processes that facilitate invasion occur in riparian zones (Richardson *et al.*, 2007), they provide a suitable test of our suggested approach.

The majority of exotic plant species along the River Murray would have been introduced after the development of large scale irrigation in the 1870s (Smith & Smith, 1990), and would have escaped from local agriculture and horticulture or been released from aquaria (Randall, 2007; Hulme *et al.*, 2008). Most of the exotic species would still be dispersal limited (Caley *et al.*, 2008), and source populations (e.g. around human settlements and agriculture), dispersal pathways (e.g. water, roads) and vectors (e.g. humans, livestock) would affect exotic species distribution in the region. The abundance and distribution of exotic flora would also reflect abiotic conditions, like hydrology and geomorphology (climatic and edaphic characteristics, elevation and water quality were similar throughout the study region), and environmental disturbance. The study wetlands were subject to disturbance by livestock (cattle) and floods, and their hydrologic regimes were altered by river regulation. All of these factors can affect invasion directly or indirectly, so their scale of variation guided the spatial scales selected for the study: reaches, clumps of wetlands, wetlands and wetland sections.

Reaches primarily differed in hydrology, impacts of flow regulation, livestock grazing intensity and their proximity to areas of human activity (e.g. towns, roads). Wetland clumps related to potential dispersal distance of hydrochores, which often disperse up to 2 km (Johansson & Nilsson, 1993; Andersson *et al.*, 2000). Although wetland and riparian species commonly use polychory (Schneider & Sharitz, 1988), hydrochory (water-borne dispersal) is influential in structuring riparian plant communities (Jansson *et al.*, 2005), so hydrochory-based patterns may nevertheless emerge. Wetlands varied in geomorphology, flood histories, grazing intensity and distance to human activities, and evidence shows that individual wetlands can have distinct community assemblages (Brock *et al.*, 2003). Even within a single wetland, there may be differences in human disturbance and grazing pressure (Jansen & Robertson, 2001) and propagule distribution (Britton & Brock, 1994), so sections of wetlands (approximate thirds) were surveyed as well. Differences in water depth among sites were largely accounted for by Depth-strata. The influence of depth on flora is well-documented (Blom & Voesenek, 1996; Casanova & Brock, 2000), so we did not test the effect of depth on wetland plants per se. We used Depth-strata to maximise sampling efficiency, reduce residual error, and examine whether the floristic patterns at the four spatial scales differed at different depths.

In floodplain wetlands of the regulated River Murray, we surveyed vegetation using a nested, crossed approach to (1) determine at which of the four spatial scales cover of species and groups of species vary, and (2) determine the scale that accounted for most variability in exotic species abundance, and infer prospective causal mechanisms based on the scale of environmental variation. We examine responses of exotic and native species groups, native weeds and 10 individual species, as well as grazing intensity and water depth. Spatial variation in species' distributions was used to examine whether species responses relate to life history and geographic origin, not to infer mechanisms of invasion. Native weeds are species that are native to Australia but are invasive in other parts of the world (Randall, 2007). A recurring hypothesis in invasion ecology is that certain traits are associated with invasiveness and successful invaders are therefore similar (Baker, 1965; Sutherland, 2004). By comparing responses of native weeds to native non-weeds and exotic weeds across four spatial scales, we test whether variation in native weed cover aligns more closely with other native species or exotic weeds. This will indicate whether it is species' weedy autecological traits that govern responses or whether exotic and native species differ for other reasons.

METHODS

Study region

Research was conducted in temporary floodplain wetlands of the regulated River Murray in south-eastern Australia (Fig. 1). The area is temperate with 400–600 mm of annual rainfall (BOM, 2005) and is underlain by alluvial deposits (Crabb, 1999) with hard-setting loamy soils and clayey subsoils (DNM, 1960). The study region has been subject to livestock grazing

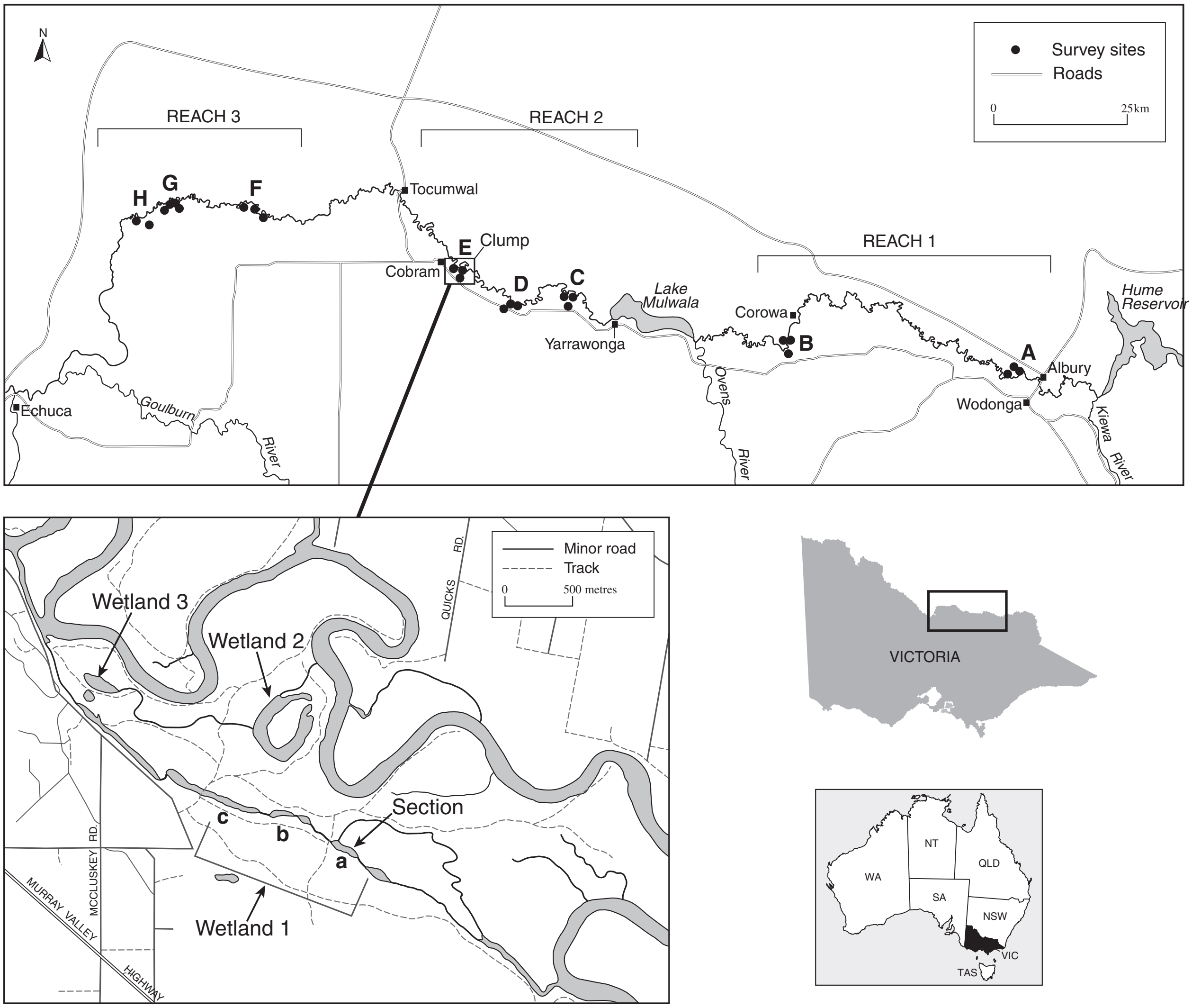

Figure 1 Map of the study region that illustrates the hierarchical design of the study with three reaches, eight clumps, 24 wetlands and 24 sections. The study area extended from 35°49′–36°5′ S and 144°59′–146°51′ E. Reaches are labelled 1–3, Clumps A–H. In the enlargement of Clump E, wetlands are labelled 1–3 (three wetlands in each clump), and sections of Wetland 1 are labelled a–c. Map created by Chandra Jayasuriya, The University of Melbourne.

(primarily cattle), salinization, cultivation and agriculture, logging, sedimentation, elevation of groundwater tables, pressure from recreation and tourism, and flow regulation (MPPL, 1990; Bren, 1993; Roberts, 2003). Around the time of field surveys, cattle grazing, nearby human activities and flow regulation posed the greatest threats to the study wetlands, and the 24 wetlands represented a gradient in pressure from each of these factors. Grazing intensity was expected to vary among reaches, wetlands and sections reflecting stocking rates and local access (Jansen & Robertson, 2001), whereas impacts from hydrological modification and human activities (represented by proximity to activities) varied among reaches and wetlands.

The study section of the River Murray can be divided into three reaches based on hydrology and channel geomorphology (Eastburn, 1990). A weir separates Reach 1 from Reaches 2 and 3. River regulation that began in the 1880s, primarily to service the local irrigation industry (MDBMC, 1995), has caused a 60% reduction in the long-term mean annual flow of the river and seasonal patterns have altered (Thomson, 1994). The most upstream reach (Reach 1) was just downstream of a major dam (Hume Dam). It has experienced almost complete reversal in flow seasonality, with high flows now occurring in summer instead of winter (Maheshwari *et al.*, 1995). Events that occurred every 20 years under pre-regulation conditions, now occur every 34 years (J. Catford, B. Downes and C. Gippel, unpublished data). The middle reach (Reach 2) receives 77% of pre-regulation flows, but its seasonal flow pattern is largely unchanged due to inflow from a largely unregulated tributary (Ovens River) (MDBC, 2005). Downstream of the Ovens River, events that occurred every 2 and 20 years before regulation now occur every 5 and 29 years, respectively. The most downstream reach (Reach 3) centres on the Ramsar-listed Barmah-Millewa Forest and has experienced an increase in small unseasonal floods and a reduction in mid-range flows (Chong & Ladson, 2003). Because the 24 study wetlands differed in their downstream location, inflow characteristics and elevation on the floodplain, the wetlands varied in hydrological characteristics and degree of hydrological modification. The flood regime and degree of hydrological modification of the study sites therefore varied at reach- and wetland-scales.

Survey design

Reaches differed in length (Table 1). Clumps, nested in reaches (two in Reach 1, three in Reach 2 and Reach 3), were randomly selected and consisted of three discrete wetlands that were within *c.* 2 km of each other. The three wetlands in each clump (24 wetlands in total) were temporary and primarily flooded by river water, and were randomly selected from a group of local wetlands. Boundaries of wetlands were defined as the point where the elevational gradient became flat and where hydrophytes stopped occurring (Sharp & Keddy, 1986). Characteristics of the study wetlands varied (Table 2), including their flood regimes and flood histories (see Walker *et al.*, 1995). The size of wetlands differed among reaches, but differences were not statistically significant (ANOVA: $P > 0.05$). Wetlands in Reach 1 were closest to the nearest town while wetlands in Reach 3 were furthest away (Table 2).

One wetland in each clump was surveyed in three sections (24 sections in total), which were haphazardly selected (no physical barriers partitioned the wetlands). Sections within each wetland were at least 20 m apart and were similar in size (Table 1). Two wetland sections were completely dry and did not contain any living vegetation. These two sites were statistical outliers with large leverage and, because they do not provide information about wetland plant communities, they were excluded from the analysis. Sections and wetlands were surveyed using the same method and, together, are referred to as study sites.

Wetlands and sections were divided into three strata based on elevation and water depth (deep, medium and shallow), which corresponded with vegetation zones at a site (Blom & Voesenek, 1996). Boundaries of the Depth-strata were site-specific, so their depth ranges were relative and overlapped among sites. Two wetlands were too shallow to decipher difference in elevation, so a fully random sampling design was carried out at these sites (24 points, no stratification).

Table 1 Definitions and characteristics of the four spatial scales used in the survey.

Study scale	Reach	Clump	Wetland	Section
Definition	Segment of river with distinct hydrology and floodplain geomorphology	Group of three wetlands hydraulically connected at some point in time	Discrete river-fed temporary water body representing a range of geomorphologic types and ages	One-third of an individual wetland, divided according to flow direction or wetland shape
Sample size	3	8	24	24 (2 excluded from analysis)
Spatial extent*	74.0 km mean ± 8.7 km SE (Reach 1, 95 km; Reach 2, 67 km; Reach 3, 60 km)	1.3 km median; 1.7 km mean ± 0.28 km SE	4.32 ha median; 7.12 ha mean ± 1.89 ha SE	2.22 ha median; 3.65 ha mean ± 0.81 ha SE
Distance between entities†	Not applicable (study area divided into three reaches)	14.6 km median; 22.4 km mean ± 3.5 km SE	1.09 km median; 1.57 km mean ± 0.23 km SE	50.0 m median; 57.0 m mean ± 10.5 m SE

SE, standard error of the mean.

*Spatial extent of each study scale in km of river distance.

†Note the different units for different spatial scales.

Table 2 Spatial distribution of 24 wetland sites.

Wetland site characteristics	Reach 1	Reach 2	Reach 3	Overall mean
Area (ha)	6.0 ± 1.42	11.0 ± 4.71	4.0 ± 1.06	7.1 ± 1.89
Median distance to river (km)	0.7 ± 0.26	0.4 ± 0.13	0.2 ± 0.05	0.4 ± 0.09
Length of primary inlet (km)	1.1 ± 0.40	1.0 ± 0.44	2.9 ± 1.51	1.9 ± 0.59
Distance to other wetlands in clump* (km)	1.3 ± 0.16	0.9 ± 0.09	2.5 ± 0.48	1.6 ± 0.23
Distance to neighbouring clumps* (km)	41.4 ± 0.31	20.0 ± 5.04	13.7 ± 3.90	22.7 ± 3.53
Distance to nearest road (km)	1.5 ± 0.78	1.5 ± 0.21	15.1 ± 1.48	6.6 ± 1.48
Distance to nearest town (km)	6.3 ± 0.61	9.48 ± 1.23	19.1 ± 0.47	12.3 ± 1.23

Values shown are mean ± standard error of the mean.

*Clump refers to group of three wetlands that were within 2 km of each other.

Floristic survey

Study sites were surveyed over an 8 week period in the austral summer (13 December 2005–4 February 2006). The cover of some terrestrial annual exotic species may have been underrepresented at the time of year surveyed, but it was the optimum time to identify the majority of wetland plant taxa due to the presence of distinguishing features (Baldwin *et al.*, 2004; Reid & Quinn, 2004), so a trade-off was made. Generally, sites within one clump were surveyed each week (order that sites were surveyed in each clump was random). Survey dates were unrelated to Reach. Vegetation was surveyed at 24 random points in each site (eight points per depth-stratum). When wetlands were surveyed as three sections, 24 random points from the 72 points surveyed were used to represent the wetland. Points were generated in a geographical information system (GIS) environment (Hawth's Analysis Tools: Beyer, 2005) based on a digital elevation model (DEM) of the River Murray floodplain (MDBC, 2001) and located in the field with the help of a geographical positioning system (GPS: 12XL, Garmin, Olathe, KS, USA; Projection: AGD66). In the few instances where GPS coverage was constrained by tree canopy, the location of the sample point was either estimated or another point surveyed.

At each sample point, a 1 m^2 square floating quadrat was blindly tossed. All taxa in the quadrat were recorded, and their foliar cover estimated using the Braun-Blanquet scale (Kent & Coker, 1992). Braun-Blanquet scale values were converted to mid-point averages for statistical analysis (+: 0.5%, 1: 2.5%, 2: 15.5%, 3: 38%, 4: 63%, 5: 87.5%) (Floyd & Anderson, 1987). Of 170 taxa recorded, 132 were identified to species-level, 147 to genera and 160 to family (Botanic-Gardens-Trust 2007; Ross & Walsh, 2007). Taxa were categorised according to geographic origin and weed status (Randall, 2007), growth form, and functional group (Brock & Casanova, 1997) (Table 3). The functional classification scheme was based on the reproductive requirements and growth responses of plant species in relation to water regime (Brock & Casanova, 1997). Native taxa are indigenous to Australia (Randall, 2007) and most likely to the study region. As such, we refer to species as either native or exotic (i.e. non-native to Australia).

Ten individual species selected for analysis were observed in all three reaches, in at least six wetland clumps, in ≥ 50% of wetlands and ≥ 40% wetland sections (Table 4). Being cosmopolitan, the 10 species provided a conservative measure of the influence of scale, and were not used to infer pathways of invasion. Other species, even if more abundant overall, were too patchily distributed to enable the effects of the four spatial scales to be statistically tested. We measured water depth (if present) in the centre of each quadrat and estimated the cover of cattle pugs (a common measure of grazing intensity: Spencer *et al.*, 1998) using the same procedure as for flora.

Statistical analysis

The floristic response variables were analysed as proportions of total cover (Table 3), except species that were analysed as absolute cover. Such relative measures detect differences in the response of one floristic variable compared to the rest of the flora, so can highlight situations where factors disproportionately affect the abundance and distribution of exotic species (Ehrenfeld, 2008). Correlation analysis with the Pearson (product-moment) correlation coefficient was used to test for collinearity among proportional cover and absolute cover of exotic and native species groups.

Floristic response variables were tested using a hierarchical analysis of variance (ANOVA; mixed, partly-nested, factorial model) with two nested and one crossed factor (see

Table 3 Details of the 20 response variables tested. All of the data were log-transformed ($\log_{10}$[observed value + 1]) for analysis.

Variable	Explanation	Notes
Total cover	Total foliar cover abundance of all plants; total can exceed 100% due to multiple layers of vegetation	Sum of %-midpoint conversions of Braun-Blanquet scale
Native cover	Combined cover of all native species	Proportion of total cover that was made up of each category. Foliar cover abundance based on %-midpoint conversions of Braun-Blanquet scale (Kent & Coker, 1992). Origin (native or exotic) and weed status according to Randall (2007). Native weeds are native to Australia but invasive in other parts of the world. Functional classification (terrestrial or amphibious) based on plant species response to flood regime (Brock & Casanova, 1997)
Terrestrial native	Combined cover of native species that inhabit the dry, terrestrial end of wetland zonation	
Amphibious native	Native species found in the wet–dry ecotone that require both inundation and drawdown	
Exotic cover	Exotic species cover	
Terrestrial exotic	Exotic species that inhabit the dry, terrestrial end of wetland zonation	
Amphibious exotic	Exotic species found in the wet–dry ecotone that require both inundation and drawdown	
Native weeds	Native weed cover	
Species (10)	10 most cosmopolitan species (found in ≥ 50% wetland sites)	Absolute cover of each species. Further details in Table 4
Measured depth	Depth measured on-site while surveying	
Grazing intensity	Cover of cattle pugs marks	A common surrogate of grazing intensity (Spencer *et al.*, 1998)

Table 4 Classification details of the 10 species analysed (the most cosmopolitan taxa in survey).

Species*	Family†	Functional group‡	Life history†	Height (m)†	Wetland presence (%)
Eleocharis acuta R. Br.	Cyperaceae	Amphibious	Perennial	0.1–0.6	83.3
Juncus ingens N.A. Wakef.	Juncaceae	Amphibious	Perennial	1.2–4.0	66.7
Myriophyllum crispatum^{w} Orchard	Haloragaceae	Amphibious	Perennial	0.25–0.6	66.7
Conyza sumatrensis§ (Retz.) E. Walker	Asteraceae	Terrestrial	Annual	0.1–2.0	62.5
Pseudoraphis spinescens (R. Br.) Vickery	Poaceae	Amphibious	Perennial	0.4–1.0	62.5
Paspalum distichum^{w} L.	Poaceae	Amphibious	Perennial	0.4–0.7	58.3
Persicaria prostrata (R. Br.) Sojak	Polygonaceae	Amphibious	Perennial	0.15–0.3	58.3
Triglochin procera R. Br.	Juncaginaceae	Amphibious	Perennial	0.15–2.0	58.3
Hypochaeris radicata§ L.	Asteraceae	Terrestrial	Perennial	0.15–0.8	54.2
Cirsium vulgare§ (Savi) Ten.	Asteraceae	Terrestrial	Biennial	0.2–1.5	50.0

^{w}Native weed; remaining are native non-weeds.

*Origin and status based on Randall (2007).

†Information from The Flora of New South Wales (Botanic-Gardens-Trust 2007); sizes of plants observed were within the bounds reported here, but did not always reach the maximum.

‡Species classification based on Brock & Casanova (1997) and Reid & Quinn (2004).

§Exotic.

Appendix S1 in Supporting Information). Measured depth and grazing intensity (cover of cattle pugs) were also analysed in this way. Reach was treated as a fixed factor, whereas Clump, Wetland and Section were random. Because we were interested in the amount of overall variability that depth explained (not the actual difference between depth strata), and because depth strata were relative and varied among sites, Depth-strata was treated as a random factor crossed with all spatial scales. All interactions were treated as random (Quinn & Keough, 2002). Two types of analyses were run – each with three spatial scales (Wetland-scale analysis: Reach, Clump, Wetland; Section-scale analysis: Reach, Wetland, Section). Wetland-scale analyses were used to examine the effect of all factors and interactions except Section and the Section*Depth-strata interaction. For simplicity, we report the combined results of both models. Full results are provided in Appendix S2 and S3.

We used the restricted version of a mixed nested factorial model to test for main effects, and for interactions of the four terms in both models (Quinn & Keough, 2002). There is debate in the statistical and biological literature about whether to use restricted (i.e. where different combinations of interactions terms can show trends, as long as they pool to zero) or unrestricted models (all combinations of interaction terms are assumed to be the same: Quinn & Keough, 2002). The restricted version (also known as constrained parameters: Voss, 1999) assumes that any two interaction terms (nested in a random factor) will co-vary, whereas the unrestricted version assumes that pairs of interaction terms are independent within each level of the factors in which they are nested (random or fixed: Quinn & Keough, 2002). Despite the names suggesting otherwise, assumptions regarding interactions are less strict for the restricted version than the unrestricted version, and Voss (1999) has argued that it is the more conservative of the two approaches. Given the high likelihood that the spatial scale factors in our study would have been spatially autocorrelated, the restricted version was more suitable for the study design.

Without an appropriate denominator to use to calculate *F*-ratios of Reach (the only fixed factor in the model), quasi *F*-ratios were used to estimate the main effect of Reach (Quinn & Keough, 2002). Because 20 response variables were tested, the probability of at least one Type I error occurring in this family of tests was 0.64 (Quinn & Keough, 2002). Although one test is likely to show significant results based on chance alone, we are examining collective patterns. Consequently, less attention is given to the *P*-values of specific tests because the focus is on general patterns.

All of the data were log-transformed ($\log_{10}$[observed value + 1]) to meet homogeneity of variance and normality assumptions. Amphibious exotic cover was patchy with low cover, and the residual plots suggest it may have violated the assumption of homogeneity of variance assumption. It should therefore be interpreted with care. All response variables had outliers, but removing them did not change the interpretation of results, except in one case (see Table 5). MINITAB 15 was used to perform all analyses (Minitab 15 Statistical Software; Minitab Solutions, State College, PA, USA). Alpha was set as 0.05 in all tests.

RESULTS

The 170 taxa recorded in the survey were from 42 families, most of which were herbs (Fig. 2a). Weeds made up 45.3% of all taxa (exotic taxa and native weeds according to Randall, 2007). Native taxa accounted for 51.1% of taxa, and 33.5% were exotic. The remainder could not be indentified to species-level, so their origin was unknown (Fig. 2b). There was a weak negative correlation between proportional cover of exotic and native species (Pearson correlation coefficient, $\rho = -0.433$, $P < 0.001$ for all correlations). On average,

Table 5 Summary of significant effects and variance components of four spatial scale factors and Depth-strata on 20 response variables from ANOVA.

Variable	R	C	W	_Sc†_	D	R^{x}D	C^{x}D	W^{x}D	_Sc^{x}D†_	Resid.
d.f.	2	5	16	_14_	2	2	10	32	_28_	504
Total cover	1	0	4	_1_	**35*****	0	6	**20*****	_10***_	35
Native weed	6	9	2	_0_	0	0	0	**27*****	**_18***_**	56
Native cover	2	0	6	_0_	13**	0	0	**27*****	_12***_	52
Terrestrial native	2	0	0	_5_	**32*****	0	2	**22*****	_11***_	41
Amphibious native	4	0	14*	_1_	3	0	0	**20*****	_12***_	59
Exotic cover	**26***	1	12**	_9**_	14***	0	0	7***	_2***_	39
Terrestrial exotic	**24**	6	11**	_14***_	**17*****	3*	0	9***	_0_	31
Amphibious exotic	1	0	3	_5_	4*	0	0	**23*****	_8**_	69
Species										
Eleocharis acuta	7	1	4	_1_	9*	1	8	**19*****	_3_	52
Juncus ingens	4	10	8	**_16***_**	1	3	7	**21*****	_4*_	46
Myriophyllum crispatum^{w}	11	2	9*	_1*_	0	0	11*	**15*****	_0_	52
Conyza sumatrensis‡	3	4	12*	_0_	0	0	0	**17*****	_1_	64
Pseudoraphis spinescens	2	**18***	11**	_7**_	8*	3	6*	6**	_5**_	47
Paspalum distichum^{w}	**21**	0	1	_10*_	1	0	0	**21*****	_11***_	55
Persicaria prostrata	0	7	0	_2*_	3	1	3	10**	_0_	75
Triglochin procera	2	4	0	_5_	1	1	0	6*	_3_	86
Hypochaeris radicata‡	0	1	9*	_0_	8*	0	6	**17*****	_7*_	60
Cirsium vulgare‡	0	0	4	_0_	3	1	2	4	**_17***_**	86
Other										
Measured depth	0	6	6*	_6*_	**60*****	0	5	13***	_7***_	11
Grazing intensity	13	10	15***	**_18***_**	15***	8*	0	10***	_10***_	30

Factors that explained > 15% of total variance are in bold.

All data were $\log_{10}$-transformed. When outliers were removed, Sc^{x}D became significant for *M. crispatum*. Full results in Appendix S2 and S3.

d.f., degrees of freedom; Factors: R, reach; C, clump; W, wetland; Sc, section; D, Depth-strata.

†All results from Wetland-scale analyses except Sc and Sc^{x}D (italics), which are from Section-scale analyses; results from the two models are not strictly comparable. α set at 0.05. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

Species: ^{w}native weed; ‡exotic.

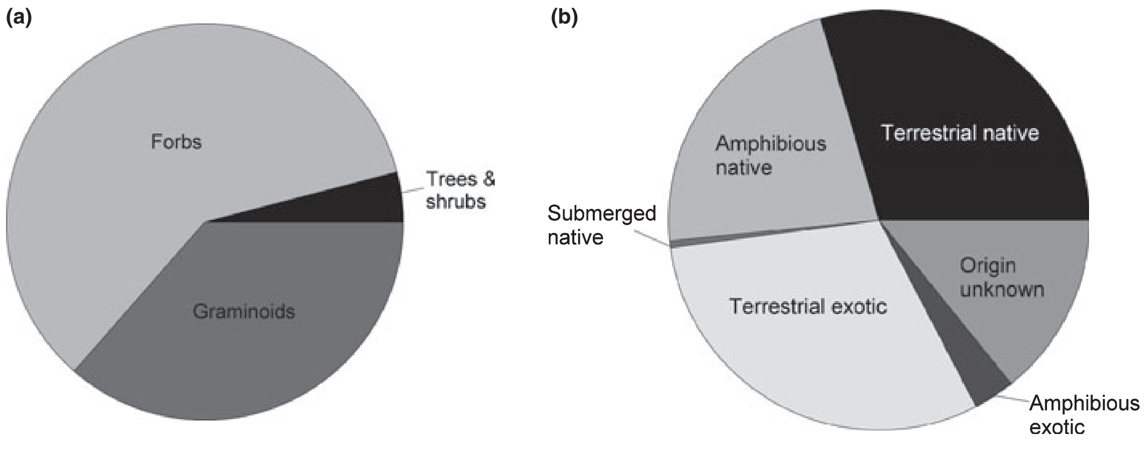

Figure 2 Proportion of taxa classified by (a) growth form and (b) origin and functional group. No exotic submerged species were recorded. Submerged species are those that germinate, grow and reproduce underwater (Brock & Casanova, 1997).

72% ± 1.4 (SE of mean) of total cover was native whereas 16% ± 1.0 was exotic. Based on growth form, phylogeny and functional characteristics, the native species group was more diverse than the exotic species group. Of the 87 native species from 31 families, 56.3% were classified as terrestrial and 54.0% forbs. The 57 exotic species from 21 families were mostly terrestrial (89.5%) with a forb growth form (70.2%). Depth-strata had a resounding and consistent effect on wetland flora (Table 5). Total cover was generally highest in shallow depth strata and lowest in deep strata, except amphibious cover that peaked in medium strata.

Exotic cover and terrestrial exotic cover varied with scale. In contrast, cover of native species groups did not, with the sole exception of the amphibious native species (Table 5; native non-weed cover followed the patterns of native cover, details not reported). Exotic cover and terrestrial exotic cover varied significantly at the Reach-, Wetland- and Section-scales. Terrestrial species dominated the exotic species pool and therefore displayed similar trends. Unlike the majority of response variables where Depth-strata accounted for most variance, exotic cover and terrestrial exotic cover varied most at the Reach-scale (Variance components: Reach > Depth-strata > Wetland > Section).

Proportional exotic cover decreased markedly from Reach 1 to Reach 3, whereas native cover was relatively constant among the three reaches (Fig. 3). Proportional and absolute exotic cover were strongly correlated ($\rho = 0.821$), and absolute exotic cover also showed a marked decrease with distance downstream (results not shown). The four spatial scales explained little of the total variance of the other group-based response variables except amphibious native cover, which varied among wetlands. Absolute cover of native species was correlated with proportional native cover (though not as strongly, $\rho = 0.527$), and neither varied significantly among the three reaches.

Some species did not vary with scale at all (e.g. *Eleocharis acuta*), whereas others varied at a few scales (e.g. *Pseudoraphis spinescens*; Table 5). Most variation in cover of the 10 species occurred at the two smaller scales, with Wetland accounting for the greatest proportion of variance. Even though six response variables varied significantly at the Wetland-scale and seven response variables at the Section-scale, the variance components indicate that Reach explained the greatest amount of variability of all of the spatial scale factors. This was largely due to variation in exotic cover and terrestrial exotic cover at the Reach-scale. Species responses were unrelated to their geographic origin, weed status, functional group or growth form. Grazing intensity and measured depth varied among Wetlands, Sections and Depth-strata (Table 5). Although grazing intensity did not vary significantly at the Reach-scale, Reach accounted for 13% of its variance. Grazing intensity peaked in Reach 2 and was lowest in Reach 3.

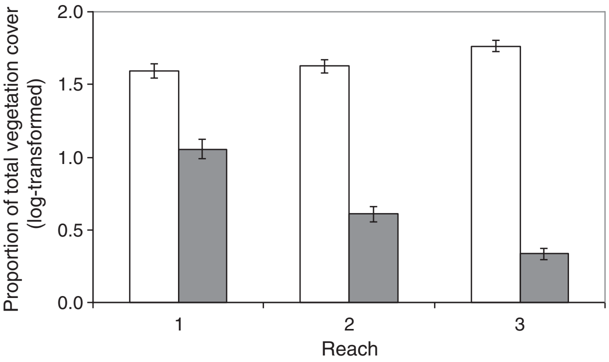

Figure 3 Mean proportional native and exotic cover in the three study reaches with standard error bars. White bars, native cover; grey bars, exotic cover.

DISCUSSION

The most notable findings from this study were the distinct responses of exotic and native groups at different spatial scales and the decrease in exotic cover from Reach 1 to Reach 3. The disparate effect of Reach, Wetland and Section on cover of exotic and native species (including native weeds) most likely stems from dispersal-limitation and the occupancy time of individual species (i.e. time since immigration or speciation), the diversity of the native and exotic species pools, disproportionate effects of livestock grazing on exotic and native vegetation and the close relationship between humans and exotic species. The extent of hydrological modification and proximity to human activities varied at Reach- and Wetland-scales, and grazing intensity and depth varied at Wetland- and Section-scales. Variation in these factors – along with propagule distribution that may have varied across all scales – may have affected exotic plant cover. In the following discussion, we suggest why native and exotic species groups differ in their responses to spatial scale, and consider factors that are likely to drive variation in exotic plant cover at the Reach-, Wetland- and Section-scales. We finish by considering the implications of our study for surveys of wetland plant communities and exotic invasion more generally.

What drives the difference between exotic and native plant distribution in the study region?

Dispersal limitation

Numerous studies have shown a positive correlation between the level of invasion and the time that has elapsed since exotic species introduction (Richardson & Pyšek, 2006). Unlike their native counterparts that may be at equilibrium, time may have been insufficient for exotic species to reach the full extent of their range. The earliest introduction of exotic species into the region would have been at the time of European settlement in the early 1800s (Jacobs, 1990), but some species may have only reached the region relatively recently [e.g. *Sagittaria platyphylla* (Engelm.) J.G. Sm. was first sighted in 1962 in a tributary of the River Murray (G-MW 2005) and, although currently undergoing rapid spread, it is still dispersal-limited (J. Catford, pers. obs.)]. Assuming that it takes about 150 years for most introduced species to reach their full range size, as has been found in South Australia (Caley *et al.*, 2008), only those introduced before 1860 (i.e. before the region was developed for large scale irrigation: Smith & Smith, 1990) would have ceased expanding their range. Even if some species can reach their full range more quickly, the range of most exotic plant species in the region would still be limited. Dispersal limitation may have caused variation in exotic cover at Reach-, Wetland- and Section-scales (Brock *et al.*, 2003).

Occupancy time and phases of invasion

Related to occupancy time, the variation of exotic cover at multiple scales may reflect that individual species are at different phases of invasion, and are thus affected by different factors that vary at different scales (Catford *et al.*, 2009). With time, propagule pressure tends to increase, which reduces dispersal-limitation (Richardson & Pyšek, 2006), and invading species may genetically adapt to the biotic and abiotic conditions of the recipient ecosystems enabling them to naturalise and spread (Joshi & Vrieling, 2005; Ricklefs *et al.*, 2008). With increased time, it is also likely that new species will be introduced into a region increasing the diversity of the exotic species pool (Eriksson, 1993). The variance we observed in exotic plant distribution in the study wetlands may thus diminish in the future (Fraterrigo & Rusak, 2008).

Diversity of exotic and native species groups

The growth form, phylogeny and functional characteristics of taxa suggested that the native species group had higher diversity than the exotic species group. Controlling for Depth-strata, the diversity and breadth of the native species pool enabled native taxa to occupy the full array of ecological conditions, as indicated by low variability in native cover at the four spatial scales. Given that species are introduced non-randomly (Colautti *et al.*, 2006), it is not surprising that the exotic species pool was less diverse, and this may have limited the type of environmental conditions they could occupy (Tilman, 2004).

Unique relationships, not traits, of invading species

The majority of exotic species were terrestrial, so may have varied at the Wetland- and Section-scale because water depth varied at these scales. However, lack of variation in cover of terrestrial natives suggests that variation in exotic cover did not stem from species' terrestrial characteristics. The distinct responses of exotic cover and native weed cover also suggest that exotic distribution was not determined by general weedy traits, which corresponds with the majority of research findings (Moles *et al.*, 2008). However, this may be an artefact of differences in their overall cover (means of 16% exotic cover and 4% native weed cover). Although certain traits do predispose plant species to being invasive (Rejmánek & Richardson, 1996), these traits are not universal among invaders or unique to them (Crawley *et al.*, 1996; Sutherland, 2004). Rather than species' functional traits, the patterns in exotic cover seemed to relate to something that only affected exotic taxa, whether that was dispersal-limitation, propagule bias and habitat preferences, livestock grazing, the foreign and novel evolutionary histories of exotic species, or the commensal relationship between exotic species and humans (Catford *et al.*, 2009). We address these now.

Factors that affected exotic plant species abundance at three spatial scales

Instead of being spread uniformly along the length of the river, exotic cover (absolute and as a proportion of total cover) was highest in wetlands in Reach 1 and lowest in Reach 3. This trend corresponds with the extent of hydrological modification caused by river regulation and proximity of human activities, and these factors may have caused variation in exotic cover at the Reach- and Wetland-scales.

By modifying environmental filters (Weiher & Keddy, 1995), long-term changes to environmental conditions, like hydrology, can alter the structure of riparian plant communities and expose the community to invasion (Johnson *et al.*, 2008; Moles *et al.*, 2008). Whereas cover of native species was unaffected, the results suggest that altered hydrological conditions may have favoured exotic species in upstream wetlands causing the longtitudinal trend observed. Because of differences in geomorphology, the extent of hydrological modification varied among wetlands as well, and may have caused variation in exotic cover at this scale. The small sample size of reaches ($n = 3$) limited our ability to rigorously test relationships at the Reach-scale, but a follow-up study indicated that hydrological modification has facilitated exotic plant invasion at the Wetland-scale, largely because of a reduction in peak flows (J. Catford, B. Downes & C. Gippel, unpublished data). Because exotic cover was dominated by terrestrial species and native cover by amphibious species, the reduction in flood magnitude and depth provided conditions that disproportionally advantaged the exotic species group.

Another explanation for the decrease in exotic cover with distance downstream relates to the proximity of human activities: upstream wetlands were closer to the nearest town, road, settlement and agricultural area than wetlands downstream. A strong association between invasion level and human population centres has been observed elsewhere (especially with recent invaders: Botham *et al.*, 2009), and probably reflects dispersal limitation (Wilson *et al.*, 2007). Intentional or not, humans are largely responsible for introduction of exotic species (Hulme *et al.*, 2008) and play a role in post-introduction dispersal (Hodgkinson & Thompson, 1997). Confirming this inference, a subsequent study revealed that exotic cover at the Wetland-scale was positively correlated to town proximity, though the relationship was not as strong as the one between flora and hydrological modification (J. Catford, B. Downes & C. Gippel, unpublished data).

Wetland-scale variation in exotic cover may also have been affected by grazing intensity and the depth of standing water. Livestock disturb vegetation and soil structure, elevate nutrient levels and act as dispersal vectors (Spencer *et al.*, 1998). Disturbance and high levels of resource availability are known to facilitate invasion (Richardson *et al.*, 2007), and previous studies have shown that livestock facilitate riparian plant invasion (Jansen & Robertson, 2001; Truscott *et al.*, 2008). Subsequent analysis (not shown here) showed that grazing intensity did not relate to proportional exotic cover at the Wetland-scale, despite a large range in intensity (24.8% mean, 22.0% SD: Catford, 2008). Water depth did not explain variation in exotic cover among wetlands either (Catford, 2008), despite its influence on wetland plants (Blom & Voesenek, 1996; Casanova & Brock, 2000). However, variation in exotic cover at the Section-scale may reflect differences in water depth and grazing intensity. Other abiotic conditions (e.g. irradiance), propagule distribution (Brock *et al.*, 2003), or effects of biotic interactions, may have been influential as well, though the latter are typically only apparent at a smaller scale where species interact (Huston, 2004). While not considered here, other factors that vary at the three scales may contribute to the floristic patterns observed.

Hierarchical surveys and study scale selection for wetland vegetation

Of the four spatial scales examined in this study, Reach accounted for the greatest amount of variance in floristic cover overall, indicating that the factors that vary at this scale are the most influential. However, its explanatory power was not consistent across response variables. Of the 20 response variables examined, only exotic cover followed the hierarchical trend where variability (as measured by variance components) is highest at the largest scale and lowest at the smallest one. Response variables mostly varied at the Wetland- and Section-scale, especially cover of individual species. While local site conditions accounted for most variation in cover of the 10 study species, Clump and Reach still accounted for > 15% variance of some species' cover. It is established that species – and groups of species – may respond to multiple factors that vary at multiple scales (Belyea & Lancaster, 1999; Maurer & Taper, 2002). However, the fact that species were affected by factors that operated at different scales, despite individual plants being similar in size, confirms the importance of studying biota, and biological communities in particular, at multiple scales (Wiens, 1989). Because wetland plant assemblages are temporally dynamic (Brock *et al.*, 2003), different patterns may have emerged if we had documented spatial variability of exotic and native vegetation at multiple times.

Floodplain wetlands are not as congruent to hierarchical partitioning as streams and rivers (e.g. Wiens, 2002; Townsend *et al.*, 2004), so selecting scales that are above or below the scale of discrete wetlands is potentially more fraught. The lack of influence of Clump compared to Reach and Wetland suggests that biological variation occurs at scales where there is variation in the physical environment, like hydrology and geomorphology. The tendency to survey wetland units therefore appears justified (e.g. Toner & Keddy, 1997; Reid & Quinn, 2004). Ecologically-meaningful scales may not always be intuitive though, as is the case with the haphazardly-defined wetland sections used in this study. Even with the major depth gradient (Depth-strata) and four spatial scales accounted for, on average, over half of response variables' variance remained unexplained (55% variance unexplained in Wetland-scale analyses, 57% in Section-scale analyses). As the range of scales used to study wetland plants would suggest (e.g. Siebel & Blom, 1998; Nicol & Ganf, 2000; Kercher & Zedler, 2004), factors and processes that operate at scales above (e.g. climate) and below (e.g. competition, herbivory) those examined here are clearly influential.

Multi-scale surveys cannot identify causal mechanisms. However, they can provide an initial assessment that identifies factors likely to be important and unimportant, and can indicate where further research should be directed. Indeed, this study has identified three spatial scales where there is a disproportionate response between cover of exotic and native species groups, and has pointed to potential causal factors. Subsequent studies confirmed the roles of hydrological modification and human activities in facilitating exotic plant invasion in the study wetlands (J. Catford, B. Downes & C. Gippel, unpublished data; Catford, 2008). To our knowledge, this study has illustrated for the first time how multi-scale surveys can be used to infer factors that drive – and limit – biological invasion. At the taxon-level, a multi-scale approach is most suited to species that are widespread, easy to detect or abundant when present – invasive exotic plants make excellent candidates. By rapidly identifying factors that may affect invasive plant species, targeted multi-scale analyses could increase ecological understanding, guide future research and inform management.

ACKNOWLEDGEMENTS

Thanks to I. Conlan, B. Hradsky, A. Glaister, S. Catford, D. Marsh, C. Catford, G. Tan, G. Vietz, E. Catford, J. Edge and N. Bainton for field assistance; R. White, M. Caldwell, K. Ward, J. Hawkins, M. Copland, T. Alexander and A. Webb for access and tours of sites. Thanks also to Marnie Collins at the Statistical Consulting Centre, The University of Melbourne for statistical advice, and Jody Gunn, Kelly Hunt, Michelle Leishman, David Strayer and Peter Vesk for feedback on the manuscript. We greatly appreciated the constructive comments made by three anonymous referees. Funding for the research was provided by an Australian Postgraduate Award, CSIRO Land and Water, the Cooperative Research Centre for Australian Weed Management, Holsworth Wildlife Research Fund, and The University of Melbourne.

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SUPPORTING INFORMATION

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

Appendix S1 The statistical design for the Wetland-scale ANOVA showing factors, degrees of freedom, multipliers, and formulas to determine estimated mean squares, variance components and *F*-ratio tests.

Appendix S2 Results of Wetland-scale ANOVA that tested the effects of Reach, Clump, Wetland and Depth-strata on 20 response variables.

Appendix S3 Results of Section-scale ANOVA that tested the effects of Section and Depth-strata on 20 response variables.

BIOSKETCHES

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Author contributions: J.A.C. and B.J.D. conceived the ideas and designed the survey; J.A.C. collected the data, analysed results and led the writing.

Editor: David Richardson