Plant Ecol (2010) 211:219–233
DOI 10.1007/s11258-010-9833-7

Alterations in flood frequency increase exotic and native species richness of understorey vegetation in a temperate floodplain eucalypt forest

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Received: 7 September 2009 / Accepted: 3 February 2010 / Published online: 12 September 2010

Abstract The delivery of environmental flows for biodiversity benefits within regulated river systems can potentially contribute to exotic weed spread. This study explores whether exotic plants of a floodplain forest in Victoria, Australia, are characterised by specific functional groups and associated plant traits linked to altering hydrological conditions over time. Permanently marked 20×20 m^2 plots from five wetland sites in *Eucalyptus camaldulensis* floodplain forest were sampled twice, first in the early 1990s (1993–1994) and then 15 years later (2007–2008). Species cover abundance data for understorey vegetation communities were segregated by season and analysed using ordination analysis. Exotic species richness was modelled as a function of site flooding history and native species richness using general linear models. Site ordinations by detrended correspondence analysis showed differential community compositions between survey dates, but native and exotic species were not clearly differentiated in terms of DCA1 scores. Most exotics belonged to functional groups containing annual species that germinate and reproduce under drier conditions. Exotics reproducing under wetter conditions were in the minority, predominantly perennial and capable of both sexual and asexual reproduction. Site flooding history and native species richness significantly predicted exotic species richness. Vegetation changes are partially structured by reduced flood frequency favouring increased abundance of exotic, sexually reproducing annuals at drier sites. Sites of low flood frequency are more sensitive to future exotic weed invasion and will require targeted management effort. Flow restoration is predicted to benefit propagule dispersal of species adopting dual regeneration strategies, which are predominantly natives in this system.

Keywords Altered hydrology · Exotic weeds · Flood disturbance · Functional traits · Vegetation change

Introduction

Floodplains are considered vulnerable to exotic species (Hood and Naiman 2000; Harris et al. 2005), due to the combined influence of intensive human exploitation, a high degree of hydrological connectivity that facilitates propagule dispersal and the high spatial and temporal heterogeneity inherent to these systems. Globally, anthropogenic alterations to floodplain hydrological regimes have frequently

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resulted in riparian species invasions (Richardson et al. 2007). However, only one previous study in the northern hemisphere has examined the impacts of exotics on intact riparian forests (Schnitzler et al. 2007). Where floodplain forests are managed with specific goals (e.g. maintaining or increasing the abundance of a particular species, or conservation of a particular community type), it is important to know which aspects of the flood regime will affect the achievement of these objectives. In native river red gum (*Eucalyptus camaldulensis*) floodplain forests of south-eastern Australia two centuries of European management, combined with severe drought in recent decades has generated concern regarding forest sustainability and alteration in community composition (Chesterfield 1986; Cunningham et al. 2009; Jurskis 2009). Since the mid-twentieth century increased river regulation and reduced burning and grazing has allowed increased red gum establishment, resulting in denser stands which transpire more water and lack resilience to drought (reviewed in Jurskis 2009). Substantial forest dieback has occurred with 70% of red gum stands within Australia's Murray-Darling Basin now considered to be in poor or declining condition (Cunningham et al. 2009).

Ultimately, it is the interaction between flooding and sediment deposition that primarily determines floodplain forest composition and succession over a range of spatial scales, creating systems that are in constant temporal flux (Poff et al. 1997). Floodplain plant communities comprise flood-adapted species which are unlikely to experience stress during flooding. However, anthropogenic modification of flow regimes can alter the degree of lateral hydrological connectivity (hydrological transport onto the floodplain), resulting in altered soil nutrients, generating bare substrate and stressing established plants (Naiman and Décamps 1997; Ward 1998). Native flood-tolerant species may lose competitive advantage over invaders and recruitment of exotics may be facilitated (Shafroth et al. 2002; Stromberg et al. 2007). Alternatively, increases in the abundance of non-flood-tolerant native species may result due to increased habitat suitability. Quantifying optimal hydrological conditions provides one potential functional measure of niche overlap between exotic and native species. Measurement of fluctuations in functional group composition over time can indicate overall alterations in trait composition of forest communities (Mabry and Fraterrigo 2008), with potential relevance for management of ecosystem processes (Quétier et al. 2007).

Established plant communities are more likely to have responded to historical flow regimes rather than current flow regimes, emphasising the importance of long-term data sets encompassing hydrological and vegetation dynamics. This study uses time-series vegetation survey data to explore the impact of changing hydrological regimes on the diversity and abundance of exotic species present within understorey communities of Barmah forest, the largest contiguous stand of river red gum floodplain forest in the world, located in south-eastern Australia and protected under the Ramsar Convention. Degradation of this floodplain forest has generated mitigation schemes (MDBC 2005), including the purchase of environmental water entitlements for flow restoration aiming to benefit biodiversity ('environmental flows'). However, the delivery of environmental flows also has the potential to distribute invasive exotic weeds within the system (Howell and Benson 2000).

We aimed to investigate shifts in plant species communities and life-history attributes in response to changes in hydrological regime occurring at Barmah Forest in recent decades. Historically, this floodplain forest was composed of a matrix of continuous river red gum (*E. camaldulensis*), interspersed with open grass plains, characterised by Moira grass (*Pseudoraphis spinescens*) at sites of higher flood frequency (Bren 1992). Recorded losses of Moira grass plains to dominant native invaders such as giant rush (*Juncus ingens*) (1,200 ha) have occurred in the forest since 1930, due to altered flood regimes (Chesterfield 1986). Between 1930 and 1991, mean annual water extraction from the major river flowing through Barmah forest, the River Murray, increased by 73%, reducing the natural mean annual flow by 50% (Thompson 1992). Alterations in the seasonality of flows due to upstream storages and releases, as well as local manipulation of regulators, have resulted in a reduced frequency of large winter/spring flood events at Barmah forest in comparison to pre-regulation conditions (pre-1929) (Bren 1988; Abel et al. 2006; VEAC 2006). Management plans for future allocation of environmental water within the forest consider a diverse range of management objectives, including the conservation of the native grass plain communities (Abel et al. 2006).

This study compares historic vegetation surveys with present day community composition to evaluate whether increases have occurred in the abundance and diversity of exotic species, whether alterations in exotic species abundance are associated with historical flood frequency at specific sites and whether exotic species possess similar or different life-history attributes to those characterizing the native community. The response to historical flood frequency was modelled for species of high management concern, including *P. spinescens*, and the dominant native invader, *J. ingens*. Finally, the potential threat of weed distribution resulting from flow restoration for biodiversity benefits is discussed.

Materials and methods

Study area

Barmah Forest (35°50′S, 145°00′E) is located in south-eastern Australia on the eastern reaches of the Murray River. The climate is semi-arid with predominantly winter rainfall (mean annual rainfall 1950–2007 = 435 mm, Bureau of Meteorology, 2007). Inputs into the River Murray are largely controlled by two major upstream storages, the Hume and Dartmouth dams, constructed in 1936 and 1979, respectively. Flows are highly regulated throughout late spring, summer and autumn each year but despite river regulation the forest still has the capacity to flood in winter and early spring (CSIRO 2008). Of recent concern is the increased incidence of shallow summer flood events (Ward et al. 1994; Chong and Ladson 2003), occurring as a consequence of operational river management to meet the needs of downstream irrigators. Irrigation water released from the Hume Dam requires a downstream travel time, during which time heavy rainfall can lead to cancellation of irrigation orders. Due to restricted channel capacity upstream of Barmah Forest (10,400 Ml day^{-1}), water already released results in overbank flooding. Unfortunately, such events occur too late in the growing season to benefit native plants and are too shallow to recharge soil water on a broad scale. Chong and Ladson (2003) quantified the proportion of days for which the forest was unseasonally flooded, observing an increase from 15.5% during pre-regulation conditions (1908–1929) to 36.5% during the time period 1980–2000.

Vegetation surveys

Initial monitoring of understorey vegetation was conducted in 1993 (Ward 1994) at five grass plain wetland sites within the forest, Boals Deadwoods, Top Island, Little Rushy Swamp, Top Lake and Steamer Plain (Table 1). At each wetland site, two 200-m transects were established, ascending from a low elevation in the open plain to a relatively higher elevation within the boundary of continuous river red gum. Transect endpoints and mid-position were marked by three 20 × 20 m quadrats for every site, with the exception of Steamer Plain, where four quadrats per transect were established, resulting in a total of 32 permanent quadrats within the forest. In 1993, understorey vegetation was surveyed seasonally in January, April, July and October. Spring and autumn surveys were timed to approximately coincide with the historically wettest (October–November) and driest phases (March–April) of the flood regime, respectively (Ward 1994). Ten 1 m^2 random plots were established within each quadrat and cover abundance of each species in each 1 m^2 plot was visually estimated. In addition, the proportion of bare ground, leaf litter and open water present within each plot was recorded using the same classification scheme. Water depth was measured whenever flooding was present in a 1 m^2 plot at the time of survey. The 32 quadrats were marked using wooden posts and relocated in 2007. All the sites were re-surveyed in 2007 and 2008 at approximately similar times of year.

Plant origin, whether native or exotic, was determined from the census of vascular plants of Victoria (Ross and Walsh 2003). Vascular plant species were classified by life history (annual or perennial) and regeneration strategy (sexual, asexual or dual), using a variety of published sources and on-line floras. Classification of taxa into functional groups was based on that of Brock and Casanova (1997) who developed a classification scheme for wetland plants in New South Wales based on appropriate hydrological conditions for germination, growth and reproduction. In this study, five functional groups are present: terrestrial-dry species (Tdr); terrestrial-damp species (Tda); amphibious fluctuation-tolerators (Ate);

Table 1 Flooding thresholds are based on those determined by Ward et al. (1994) and represent the flow (megalitres (ML) day^{-1}), as recorded in the Murray River at Tocumwal required to produce inundation at each wetland site (commence-to-fill, CTF)

Site Latitude and longitude	Quadrat	Elevation (m a.s.l.)	Quadrat flood threshold (CTF) (Ml day^{-1})	% Flow > CTF (site flooding history) 1974–1994	% Flow > CTF (site flooding history) 1988–2008
Boals Deadwood	1.1	96.37	16,650	20.3	14.5
35°51′S, 145°01′E	1.2	96.39	16,950	20.0	14.4
	1.3	96.66	25,300	14.9	9.5
	2.1	96.37	16,650	20.3	14.5
	2.2	96.37	16,650	20.3	14.5
	2.3	96.47	21,400	16.7	10.9
Top Island	1.1	96.19	16,400	20.4	14.9
35°53′S, 144°59′E	1.2	96.21	16,700	20.2	14.4
	1.3	96.64	25,000	15.0	9.5
	2.1	96.12	16,400	20.4	14.9
	2.2	96.26	17,500	19.4	13.6
	2.3	96.49	21,650	16.6	10.8
Little Rushy Swamp	1.1	95.70	17,800	19.2	13.4
35°53′S, 145°02′E	1.2	95.70	17,800	19.2	13.4
	1.3	95.95	23,900	15.4	9.9
	2.1	95.70	17,800	19.2	13.4
	2.2	95.70	17,800	19.2	13.4
	2.3	95.98	25,000	15.0	9.5
Top Lake	1.1	94.41	9,150	58.5	57.1
35°54′S 145°02′E	1.2	94.88	13,350	25.1	20.1
	1.3	95.47	32,200	12.2	7.7
	2.1	94.52	9,700	53.1	53.2
	2.2	94.85	13,050	25.5	21.0
	2.3	95.71	53,350	5.5	2.8
Steamer Plain	1.1	95.29	8,300	65.7	63.9
35°56′S 144°59′E	1.2	95.38	8,900	60.6	60.0
	1.3	95.43	9,200	58.1	57.0
	1.4	95.62	10,550	43.6	35.1
	2.1	95.16	7,800	69.9	67.4
	2.2	95.16	7,800	69.9	67.4
	2.3	95.31	8,600	63.0	61.5
	2.4	95.76	11,700	30.0	26.1

amphibious fluctuation-responders, morphologically plastic (Arp); and amphibious fluctuation-responders, floating leaves (Arf).

Values for native and exotic species richness were obtained by counting the presence of individual species per 20 × 20 m quadrat per survey date. Alterations in the proportional frequency of native versus exotic species over time were obtained at the same scale by counting the number of times a species was recorded as present during each season for each survey date.

Historical flood regime

The topography of each 20 × 20 m quadrat was surveyed by Dumpy Level to assist in estimating individual quadrat flood regimes. Flooding thresholds (commence-to fill (CTF) values) for each quadrat represent the flow rate (Ml day^{-1}), as recorded in the Murray River at Tocumwal for which water commences-to-flow into that quadrat (Table 1), obtained from previous studies (Ward et al. 1994). Following Reid and Quinn (2004), historical daily flow data from the Tocumwal hydrograph was used to determine the percentage of days in the 20-year period before each survey that Murray flows exceeded individual quadrat CTF values, providing an estimate of flooding history for each of the five sites (Table 1). The 20-year period before 2007 and 2008 differed by only one year, and the percentage of days flooded was similar for the two alternative years, producing identical results presented in Table 1.

Statistical data analysis

Ordination with Detrended Correspondence Analysis (DCA), a form of indirect gradient analysis, was conducted with CANOCO (version 4.5 Microcomputer Power, Ithaca, NY). Plant communities at Barmah Forest are relatively unstudied, and therefore an unconstrained ordination technique was chosen due to the potential for unmeasured environmental variables contributing to species composition. All ordinations were performed using the mean species cover values per site, calculated from quadrat data, and mean values per site for each environmental variable, segregated by season. Species data were log transformed, and rare species were downweighted. Primary axes gradient lengths ranged from 4.7 to 6.6 S.D. units, justifying the use of unimodal models (Lepš and Šmilauer 2003). Pearson product–moment correlations were used to examine the relationship between DCA axis 1 (DCA1) sample scores and environmental variables.

Alterations in exotic species richness were examined on spatial and temporal bases using general linear models (GLMs). Initially, correlations between exotic and native species richness were made on data segregated by survey date, before constructing GLMs. On an individual site basis, exotic species richness was the response variable and site flooding history (Table 1) a random predictor in GLMs with identity link functions and normal errors. Native species richness was entered as a covariate. In addition, a second analysis was conducted with data pooled among sites and years to increase the ranges of the predictor variables.

The response to historical flood frequency was modelled for the dominant native, *P. spinescens*, and the native invader, *J. ingens*, using general additive modelling (GAM). In GAM, response variables are related to the predictor using semi-parametric smoothing functions that do not have fixed shapes. A log-link function was used, and since the data set consists of proportional abundance data, Poisson distribution was expected for model residuals. Survey data indicated that whilst the presence of *J. ingens* tends to be fairly constant throughout the year, peak abundance of *P. spinescens* occurs in spring and autumn (Ward 2007), and GAM models were constructed for these seasons using site flooding history as the predictor. Modelling was conducted in the CanoDraw package (version 4.5 Microcomputer Power, Ithaca, NY) and the maximum number of degrees of freedom for the smoother term was set to 2.

Results

A total of 70 plant taxa were recorded during the 1993 survey, comprising 52 (74%) native and 18 (26%) exotic species. In 2007, these values had altered to a total of 103 taxa with 65 native (66%) and 35 exotic species (34%). The total number of taxa recorded and the proportions of exotic and native taxa found in 2008 were identical to the previous year, although the taxonomic identity of exotics differed between 2007 and 2008.

Has plant community composition changed over the survey period?

The first DCA axis in the seasonal ordinations accounted for 12, 10, 9 and 9% of the total species variability for summer, winter, spring and autumn, respectively (Table 2). Site ordinations for data collected in summer, winter and spring showed differential clusterings between the early 1990s and 2007 and 2008 (Fig. 1), albeit with a degree of overlap in species composition of sites between the survey dates, particularly for the latter two years. However, the analysis for data surveyed in autumn (not shown) did not display any distinct clustering

Table 2 Correlations of environmental variables with DCA axes I and II for site ordinations conducted on a seasonal basis

Environmental correlation with DCA axes	Axis I	Axis II
Summer		
% Bare ground	−0.126	0.181
% Leaf litter	0.458***	0.647***
% Open water	−0.143	−0.100
Water depth	−0.189	−0.418***
Site flooding history	−0.440***	−0.322**
Elevation	0.691***	−0.177
DCA analysis summary		
Eigenvalues	0.873	0.565
Lengths of gradient	6.287	4.425
Cumulative percentage of variance explained: Species	11.9	19.7
Winter		
% Bare ground	0.285**	0.040
% Leaf litter	−0.430***	−0.557***
Site flooding history	0.434***	0.195
Elevation	−0.766***	−0.017
DCA analysis summary		
Eigenvalues	0.791	0.530
Lengths of gradient	4.776	5.247
Cumulative percentage of variance explained: Species	10.0	16.6
Spring		
% Bare ground	0.194	0.537***
% Leaf litter	−0.431***	0.313*
% Open water	0.181	−0.045
Water depth	0.153	−0.016
Site flooding history	0.452***	0.322*
Elevation	−0.674***	−0.208
DCA analysis summary		
Eigenvalues	0.831	0.552
Lengths of gradient	6.152	4.093
Cumulative percentage of variance explained: Species	9.1	15.2
Autumn		
% Bare ground	0.251	0.224*
% Leaf litter	−0.409***	−0.226*
Water depth	0.291**	0.147
Site flooding history	0.446***	0.178
Elevation	−0.825***	−0.344**
DCA analysis summary		
Eigenvalues	0.855	0.617
Lengths of gradient	6.664	5.212
Cumulative percentage of variance explained: Species	8.8	15.1

Results are statistically significant where indicated by *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

of sites by survey date. DCA1 did not consistently represent a temporal gradient with sites segregating along this axis according to survey period, although some temporal segregation along DCA1 is observed for the summer and spring ordinations, respectively (Fig. 1a, c).

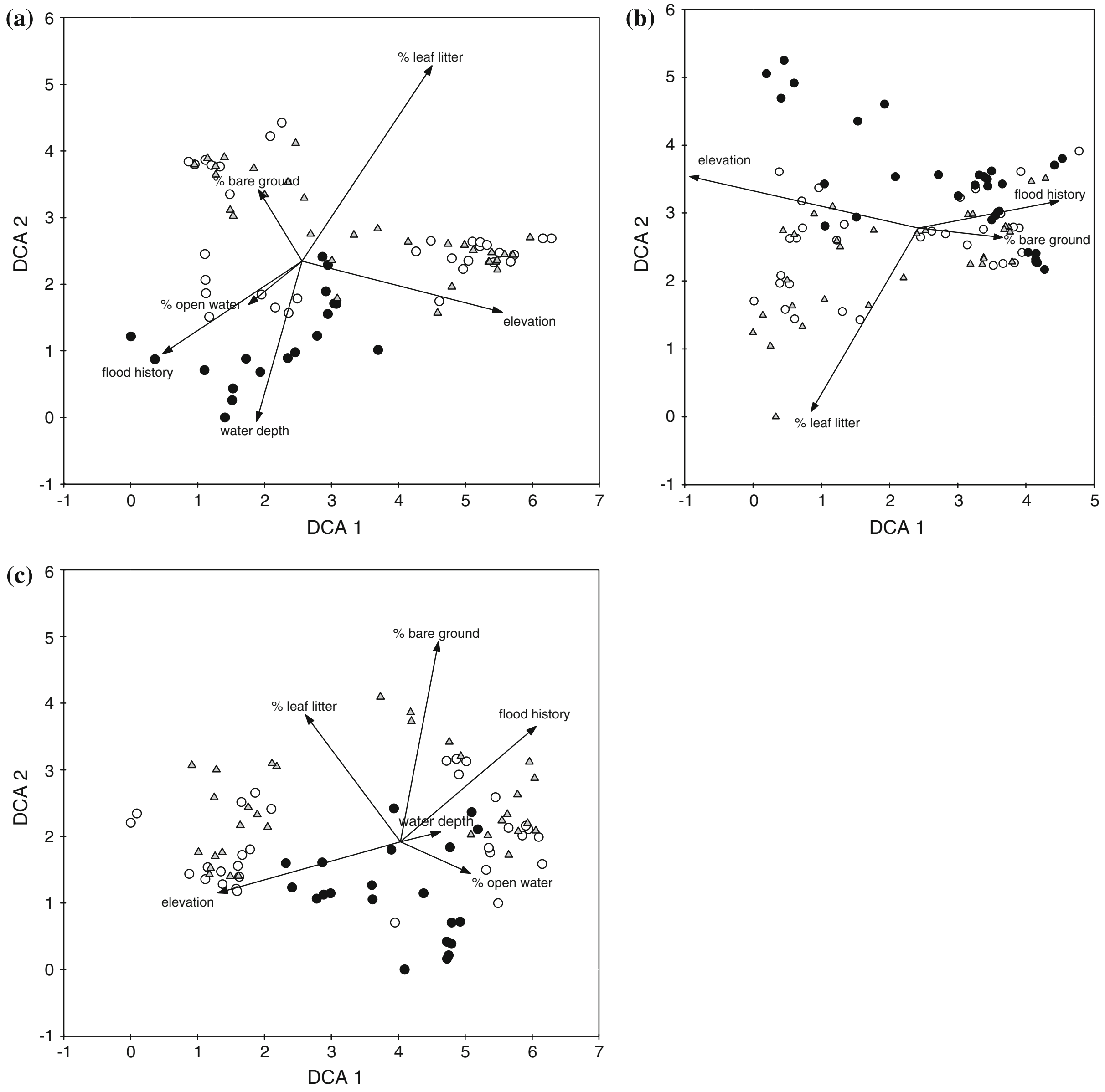


Fig. 1 DCA site ordination of understorey vegetation in Barmah Forest, Victoria, Australia for data collected in 1993 (*filled circle*), 2007 (*open circle*) and 2008 (*filled triangle*) for five wetland sites in **a** summer, **b** winter and **c** spring

Are community changes over time associated with site flooding history?

In all seasons, DCA1 scores were most highly correlated with elevation, site flooding history and the percentage of leaf litter (Table 2). Site flooding history is negatively correlated with elevation for all sites ($r = -0.59$, $P < 0.001$), imposing a temporal gradient of flooding frequency on the spatial elevation gradient, with lower elevation sites experiencing more frequent flooding over time (Table 1). Correlations of the environmental variables with DCA2 scores are more variable between seasons and reflect seasonal cycles. For example, in spring, the proportion of bare ground is highly correlated with DCA2 (Table 2), possibly providing colonisation substrate

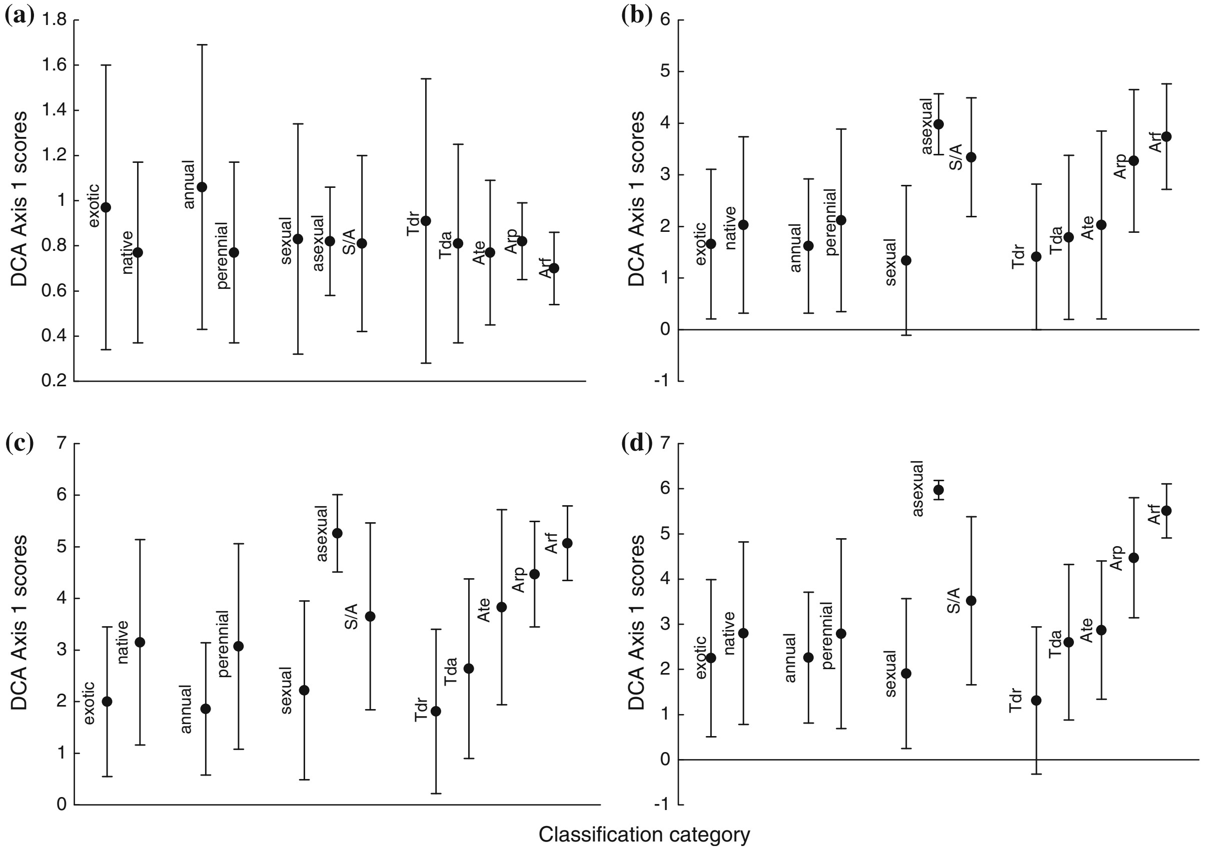


Fig. 2 Mean DCA axis I species ordination scores (±SD) for plant origin, life-history and regeneration strategy for **a** summer, **b** winter, **c** spring and **d** autumn

for an influx of previously unrecorded species, which may differentiate communities from those associated with lower DCA2 scores (Fig. 1c).

Do exotic species segregate along ordination axes according to life-history or regeneration strategy?

The species ordinations generally showed a wide range of scores on DCA1 for both native and exotic species and life-history categorisation (Fig. 2), although slight differentiation was apparent between each categorisation grouping during each season. A greater degree of differentiation was observed within the regeneration strategy category; species differed in their location on DCA1 depending on classification as either sexual or asexual in winter, spring and autumn. Species locations within the ordinations also appear to be related to functional groups, with a distinct trend in the range of DCA1 axis scores apparent in each season (Fig. 2). Differences in the number of species assigned to groups within categories bias the observations reported above. Nevertheless, it is apparent that exotic species tend to share the same range of DCA1 scores as species which are classified as annual, sexually reproducing and belonging to the drier end of the spectrum of functional groups (Tdr and Tda).

Have the proportions of native and exotic species in different functional groups altered over time?

The proportion of exotic species belonging to terrestrial-dry (Tdr), terrestrial-damp (Tda) and amphibious fluctuation-tolerator (Ate) groups generally increased from 1993 to 2008 (Fig. 3). No exotic species classified in the morphologically plastic (Arp)

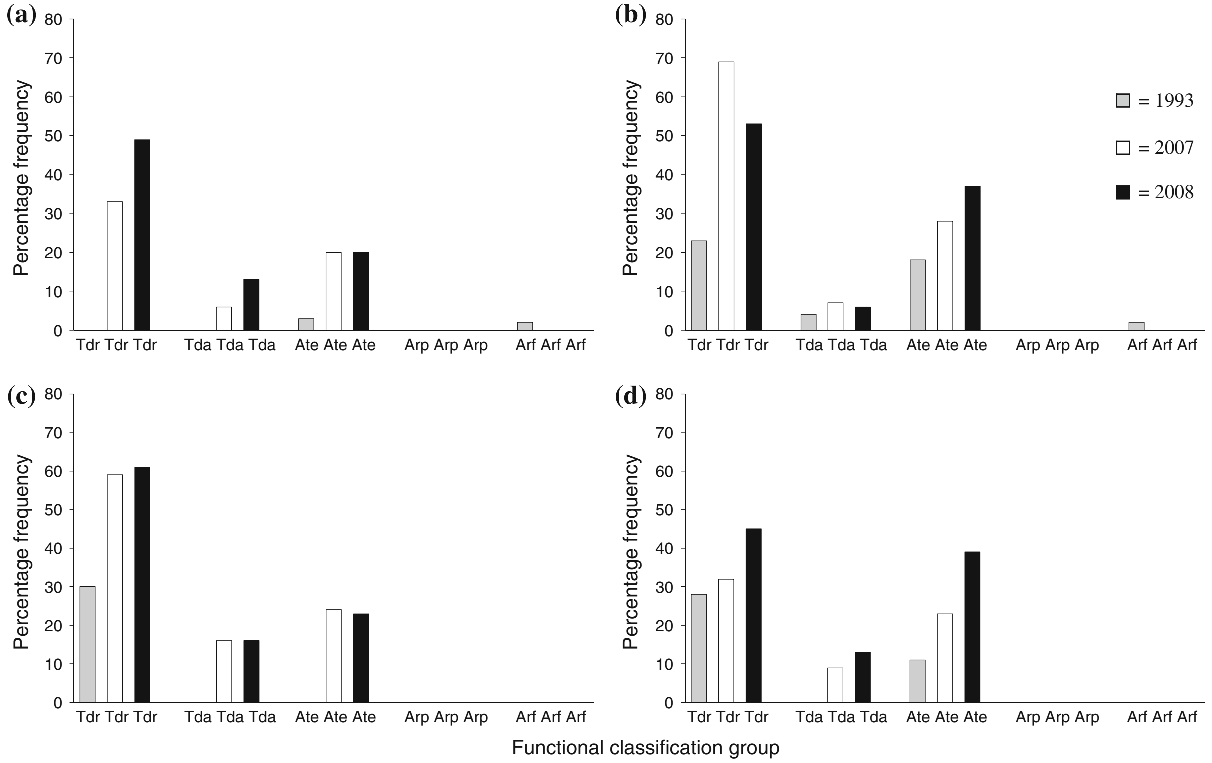


Fig. 3 Percentage composition as classified by functional group between the different survey dates for exotic species in **a** summer, **b** winter, **c** spring and **d** autumn

functional group were recorded. A small proportion of exotic species (2%) were recorded as present in the floating-leaved (Arf) functional group during summer and autumn 1993, although this value had decreased to zero representation by 2007. Representation of exotic species in the Tdr group was generally greatest in winter and spring (Fig. 3b, c), whereas exotic species in the Ate group had the highest frequencies in winter and autumn (Fig. 3b, d). Patterns of representation between seasons for the other functional groups were similar. Native species also showed alterations in proportional functional group representation over time: increases in the proportional number of natives recorded in the Tdr and Tda groups were observed in 2008 compared to the earliest survey date, whereas proportional native representation in the Arp and Arf groups declined over time (Fig. 4). The majority of the exotic species belonging to the Tdr and Tda functional groups were annual species which reproduced sexually (Table 3). However, exotic species belonging to the Ate and Arf functional groups were predominantly perennial and capable of both sexual and asexual reproduction. The pattern for native species was more variable, with a higher proportion of perennial species present within the Tdr and Tda groups in comparison to exotics (Table 3).

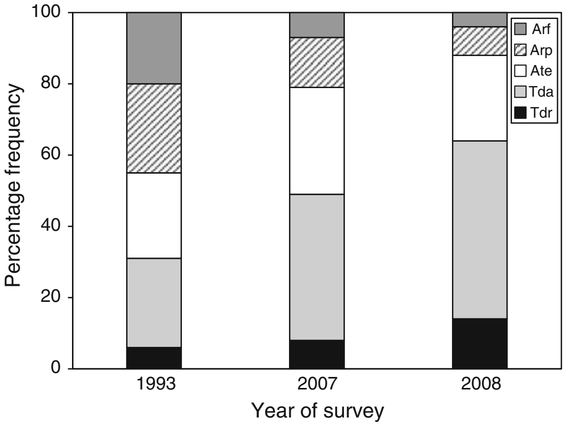
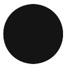
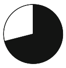
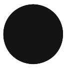
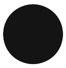
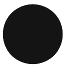
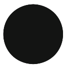
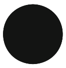
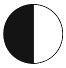
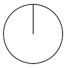
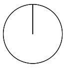
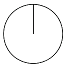
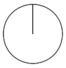
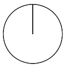
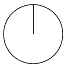
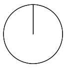
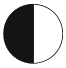
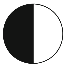
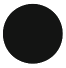
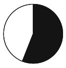
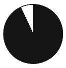
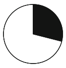
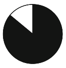
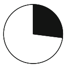
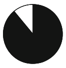
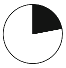
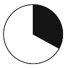
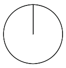
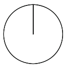
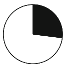
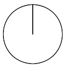
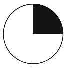
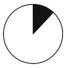
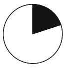
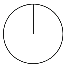
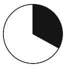
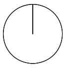
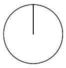
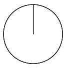
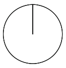
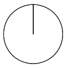
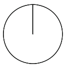
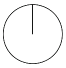


Fig. 4 Percentage composition as classified by functional group type for native plant species at Barmah Forest over the survey period

Table 3 Proportional representation of differing regeneration strategy (R, black = sexual, white = sexual and asexual) and life-history strategies (LHS, black = annual, white = perennial) observed for exotic and native species recorded at Barmah Forest between 1993 and 2008

Functional group	1993		2007		2008	
	R	LHS	R	LHS	R	LHS
Exotics Tdr						
Exotics Tda						
Exotics Ate						
Exotics Arf			NA		NA	
Natives Tdr						
Natives Tda						
Natives Ate						
Natives Arp						
Natives Arf						

Data from all seasons are combined

Can alterations in native and exotic species richness over time be predicted from site flooding history?

At the 20 × 20 m quadrat scale exotic and native species richness are generally positively correlated, with a higher correlation coefficient obtained from data collected in 2007 ($r = 0.62$, $P < 0.001$), and 2008 ($r = 0.63$, $P < 0.001$), compared to 1993 ($r = 0.37$, $P < 0.05$). Increases in exotic species richness are apparent at all wetland sites surveyed except Top Lake (Fig. 5). Temporal increases in exotic species richness cannot be attributed to alterations in site flooding history for the 20 years before the survey dates at individual sites, possibly because the measured range of hydrological changes at individual sites was limited. For example, at Top Lake, there was little alteration in flooding frequency between the survey dates at the lower elevation sites (Table 1). However, when examining hydrological data for specific years differences in inundation are discernible. For example, in 2007, inundation at Steamer Plain occurred for 3–10% of days throughout the year, dependent on quadrat elevation, whereas during 2008, conditions were very dry and no inundation occurred, possibly accounting for the sudden increase in exotics at Steamer Plain in 2008. Increases in native species richness are less prevalent

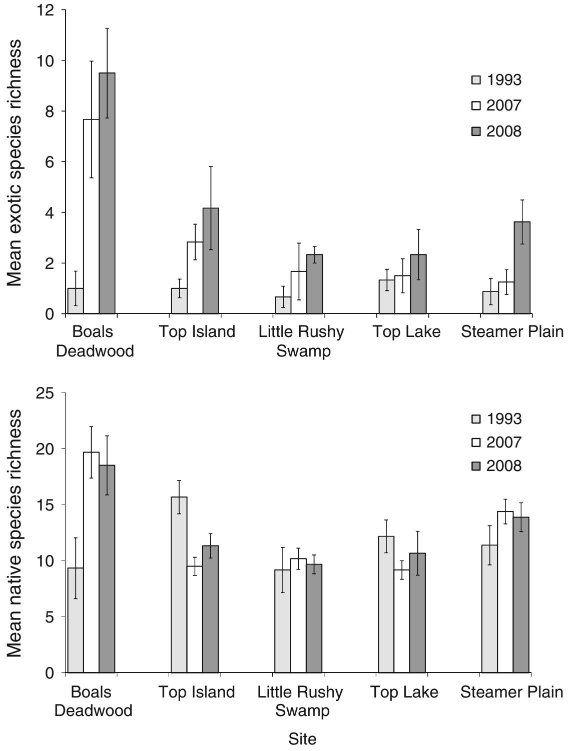


Fig. 5 Mean changes in exotic and native species richness (±1 SE) over the survey period measured at the 20 × 20 m^2 quadrat scale for each wetland site

Table 4 General linear models for exotic species richness at all wetland sites

Model	*B* (±SE)	df	*F*-ratio	*P*
Exotic species richness (all years, all sites)				
Site flooding history	−3.20 ± 1.03	44	2.03	<0.01
Native species richness	0.43 ± 0.08	1	29.44	<0.001
Error		50		
Total		95		

B shows the direction and magnitude of the effect of predictor variables. Native species richness was entered as a covariate

but occur at Boals Deadwood and Steamer Plain, which represent the driest and wettest sites, respectively. At the Top Island site, an increase in exotic species richness is observed concurrently with a decline in native species richness (Fig. 5). Combining sites within the analysis increased the range of both response and predictor variables, resulting in both site flooding history and native species richness significantly predicting exotic species richness (Table 4).

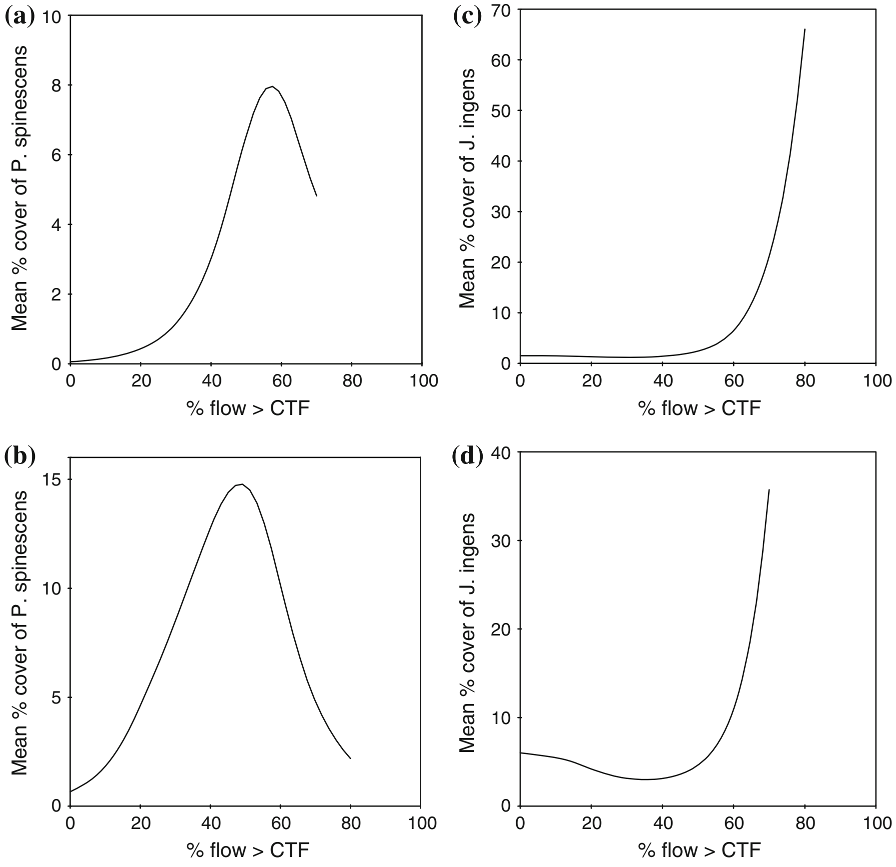
Can site flooding history predict the abundance of species of high management relevance?

The GAM response curves for *P. spinescens* indicated that optimal abundance is achieved at sites which experienced historical flooding approximately 40–60% of the time over the 20 years before the survey, with declines in abundance where proportional flood frequency exceeded 60% (Fig. 6). *J. ingens* achieves optimal abundance at sites which experienced historical flooding on 70% or more days over the time period before the study, indicating this native invader will be more prevalent at low lying areas such as Steamer Plain (Table 1), which have a higher probability of experiencing unseasonal flooding.

Discussion

The floristic communities of wetland sites in this seasonally flooded forest altered in composition over the survey period (1993–2008) but the underlying environmental gradients structuring this alteration remain unclear. Whilst DCA1 is significantly correlated with site flooding history (Table 2), the gradient in flood history between sites is not extreme (Table 1), similarities among the three less frequently flooded locations (Boals Deadwoods, Top Island and Little Rushy Swamp) contrasting with the more frequently flooded sites (i.e. Top Lake and Steamer Plain). In addition, although a decreasing trend in flood frequency from the 1990s to 2007/2008 has been observed at virtually all the sites, the gradient of flood frequency across sites was similar before both time periods (Table 1). Finally, exotic and native species cannot be separated easily on DCA1 (Fig. 2), indicating that gradients other than that represented by DCA1 (i.e. flooding history) are important in structuring their distributions. In riparian forests, tree cover is frequently important in structuring understorey vegetation (Dexter 1978). Gradients in proportional leaf litter provide an indication of the degree of tree cover and are consistently positively correlated with DCA1 (Table 2). An unmeasured variable potentially driving species composition is soil nutrient content, possibly influenced by the rate of decomposition processes resulting from

Fig. 6 The response of *P. spinescens* and *J. ingens* to site flooding history defined using Generalised Additive Models for **a** *P. spinescens*, autumn data ($P < 0.01$), **b** *P. spinescens*, spring data ($P < 0.001$), **c** *J. ingens*, autumn data ($P < 0.001$) and **d** *J. ingens*, spring data ($P < 0.05$)



interactions between the type of leaf litter and flood frequency.

Over the time period of the survey, increases in the proportional representation of exotic species at the community level were apparent for the Tdr, Tda and Ate functional groups (Fig. 3), whereas native species representation increased in the Tdr and Tda functional groups (Fig. 4). In general, the frequency of flows decreased over the study period, creating an environment increasingly suitable for plants adapted to drier conditions, including exotic annual weeds, which has potential consequences for the conservation of Moira grass plains. Increased representation of exotic flora in soil seed banks may alter the composition of regenerating plant communities following floods. Recent studies that assess seed banks of degraded floodplain wetlands in Australia to determine their contribution to wetland rehabilitation (Casanova and Brock 2000; Nias et al. 2003; Nicol et al. 2003; Robertson and James 2007; Williams et al. 2008) collectively report establishment of exotic species during dry phases of the flooding cycle. An appropriately timed flood of sufficient depth and duration may eliminate the ability of exotic annuals to germinate and/or establish. However, this strategy is necessarily dependent on both the longevity of exotic seed banks and the temporal availability of water within the system, a factor limited by high uncertainty.

The relative dominance of large-scale and local-scale drivers in controlling exotic species abundance at Barmah forest is difficult to identify. A previous spatial analysis (Robertson and James 2007) in the Kanyapella Basin (approximately 6 km south-east of Barmah forest) compared soil seed bank composition and distribution to extant wetland plant communities, concluding that seeds for most taxa were highly spatially dispersed, in contrast to the more localised distribution of many plant species in the extant vegetation. Such results indicate that seed dispersal is not limiting establishment and community composition is filtered by the spatial and temporal distribution of regeneration niches. However, the applicability of these results to the Barmah situation is unclear. What is apparent at Barmah is the existence of a positive relationship between native and exotic species richness at the 20×20 m^2 quadrat scale (Table 4), suggesting that environmental suitability and propagule supply are of greater importance than competitive interactions in structuring local-scale wetland plant communities. However, the relative importance of large-scale flood events in distributing propagules and structuring the temporal and spatial availability of recruitment niches is unknown.

The different representation of exotic and native functional groups within the forest has consequences for propagule supply and ultimately the regeneration of communities. Long-distance hydrochorous propagule dispersal of both buoyant and non-buoyant seed and vegetative fragments is known to occur during high flow events (Boedeltje et al. 2004; Truscott et al. 2006; Gurnell et al. 2008). Propagule pressure has been demonstrated as the dominant factor controlling invader establishment success in riparian forest systems of North America (Von Holle and Simberloff 2005). However, at Barmah Forest, it would be expected that the interaction between propagule pressure and hydrochorous dispersal benefits native species rather than exotics, because natives predominate in the amphibious fluctuation-responder (Arf and Arp) functional groups (Fig. 3), which are chiefly composed of species adopting the dual strategy of dispersal by both vegetative fragments and seeds (Table 3). Dual dispersal modes increase the time frame within which regeneration can take place. For example, the timing and length of the seed release period for aquatic plants often coincides with seasonal flood events (Mahoney and Rood 1998; Stokes 2008) but fragmentation can occur in a more opportunistic fashion in response to unseasonal high-flow events, enhancing overall rates of propagule dispersal. Future reductions in regional water availability in the Murray system are expected to result from a warming regional climate and increased water extraction (CSIRO 2008), suggesting that future floods at Barmah Forest will occur with reduced frequency, with potential negative consequences for the widespread dispersal of native plant propagules.

Survey data revealed that exotics with dual regeneration strategies mainly occur in the amphibious fluctuation-tolerator (Ate) group (Table 3), predominantly in autumn and winter (Fig. 3). The proportional frequency of native species within this group has remained consistent over the study period (Fig. 4), despite declines in the frequency and duration of winter floods (VEAC 2006; Abel et al. 2006). The native invader *J. ingens* also belongs to this group and has become increasingly predominant as a result of unseasonal flooding of low elevation areas. It is clear that, without remedial action, inappropriate flooding regimes will continue to result in replacement of the dominant native *P. spinescens* by *J. ingens*. The consistent representation of species within the Ate group suggests that these species are the most resilient to a range of wetting and drying patterns in terms of their ability to germinate, grow and reproduce. Future changes in the variability of flooding and drying cycles are likely to favour this group in comparison to those situated at the extreme ends of the flooding gradient.

In the context of restoring environmental flows, the low incidence of exotic species with dual reproductive strategies in our data set does not preclude a small number of species from becoming increasingly problematic in Australian floodplains. This potential risk must be evaluated in terms of the currently degraded state of the native *E. camaldulensis* stands (Cunningham et al. 2009), and the overall functioning of the ecosystem as a whole. The potential for inappropriate flooding regimes to act in concert with other management practices must also be considered. For example, Moira grass plains have been grazed by cattle since approximately 1880 (Bren 1992), and the cessation of cattle grazing is recent (March 2007, Keith Ward, pers. comm.). Grazing and trampling by livestock contributes significantly to post-recruitment mortality for native river red gums (Robertson and Rowling 2000) but the impacts on exotic species are relatively unknown. Cattle may substantially contribute to the successful recruitment of plants by trampling seed to shallow depths in soft ground, forming shallow, steep-sided depressions (pugs), which store water for greater periods of time than unmarked soil during dry periods, creating microsites of greater flood duration which may be differentially exploited by recruiting species. A previous study (Lunt et al. 2007) examining the effects of grazing exclusion on degraded understorey vegetation in riparian eucalypt forest found no effect on native or exotic species richness, despite minor compositional changes of common exotic species in ungrazed plots. The authors consider the impacts of grazing exclusion to be minor and transient but caution that results are site specific and cannot be extrapolated to less-degraded riparian systems (Lunt et al. 2007). The potential impacts of grazing exclusion at Barmah Forest are currently difficult to predict because they are confounded with alterations in hydrology, highlighting the need for broad-scale management incorporating potential interactions between different structuring factors.

To date, soil cores from red gum forests have revealed changes following European settlement such as reduced fire, increases in soil organic matter content, increased densities of eucalypts and some shrubs, and reductions in sedges, rushes and chenopods (Kenyon and Rutherfurd 1999). Floodplain forests are subject to localised heterogeneity in both soil oxygen and nutrients, due to periodic saturation and development of anoxic conditions during the growing season (Neatrour et al. 2007). Whilst both soil oxygen and nutrient content of the soil are linked to the flood cycle, the increase in exotic species could impact upon these resources due to alterations in leaf litter decomposition processes between exotic versus native species (Schulze and Walker 1997; Shah and Dahm 2008). Future research should attempt to quantify the ecosystem-level impacts of changes in plant community composition to effectively evaluate whether exotic species pose a threat to sustainability of floodplain eucalypt forest.

Conclusions

From a long-term perspective, the functional groupings of species presented here provide an indicator of underlying flood regimes which may be used to formulate spatially targeted management strategies to buffer Barmah forest from weed invasion during drought periods, a method which is applicable to flow restoration programs in other global regions. Site flooding history and native species richness were both successful predictors of exotic species richness, implying that sites of low flood frequency are more sensitive to future exotic weed invasion and will require targeted management effort. To summarise, alterations in the diversity and abundance of exotic understorey species at Barmah Forest is partially structured by reduced flood frequency favouring increased abundance of exotic, sexually reproducing annuals at drier sites. Ultimately, these alterations in community composition derive from land-use legacy, and the challenge facing us is to predict future species assemblages in a system where water resources are insufficient to recover natural flood regimes.

Acknowledgments This study was funded by Land and Water Australia under their ’Defeating the Weed Menace’ programme. Many thanks to Paula Ward for assistance in the extensive data collection.

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