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Nurse plant effects of a dominant shrub (*Duma florulenta*) on understorey vegetation in a large, semi-arid wetland in relation to flood frequency and drying

Cassandra S. James, Samantha J. Capon & Gerry P. Quinn

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Competition; Drought; *Duma florulenta*; Facilitation; Flooding; Lignum; *Muehlenbeckia florulenta*; Shrubland; Species diversity; Vegetation dynamics

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James, C.S. (corresponding author, cassandra.james@jcu.edu.au),[1]
Capon, S.J. (s.capon@griffith.edu.au),[2]
Quinn, G.P. (gerry.quinn@deakin.edu.au)[3]

[1]Centre for Tropical Water & Aquatic Ecosystem Research (TropWATER), James Cook University, Townsville, Qld 4811, Australia;
[2]Australian Rivers Institute, Griffith University, Nathan, Qld 4111, Australia;
[3]School of Life and Environmental Sciences, Deakin University, Warrnambool, Vic. 3280, Australia

Abstract

Questions: Do nurse plant interactions significantly influence understorey vegetation diversity in a large, semi-arid, shrub-dominated wetland? How do the modes and net effects of nurse plant interactions vary spatially along a flood frequency gradient, and temporally in response to drying?

Location: Narran Lakes Ramsar site, New South Wales, Australia.

Methods: Microhabitat characteristics, understorey vegetation and germinable soil seed banks were investigated in shrub and open habitats across a flood frequency gradient in a large, semi-arid wetland dominated by open shrubland under productive conditions following floodwater recession and again following 6 mo of drought. Split-plot ANOVA and multivariate analyses were used to determine the effects of shrubs on microhabitat character, understorey vegetation cover, species diversity, richness and composition and germinable soil seed banks.

Results: Microhabitat characteristics, including canopy cover, litter cover and soil character, all differed between shrub and open habitats, especially in the most frequently flooded sites. Under productive conditions following flooding, lignum shrubs suppressed understorey vegetation cover but increased species richness at the site scale across the flood frequency gradient and, in the most frequently flooded sites, supported higher species density at a microhabitat scale. Under dry conditions, lignum shrubs had a positive effect on understorey vegetation cover, species richness and species density across the flood frequency gradient, but particularly in frequently flooded sites. A significant difference in soil seed bank composition between shrub and open habitats was only observed in frequently flooded sites.

Conclusions: Nurse plant interactions appear to play an important role in determining understorey vegetation diversity in the lignum shrubland of the Narran Lakes wetland system. The modes and net effects of these nurse plant interactions vary in space and time in relation to flood history and drying. Positive interactions, probably involving microhabitat amelioration, appear to be particularly important to plant diversity and abundance under dry conditions. Under more favourable wetter conditions, lignum shrubs also contribute to understorey vegetation diversity by facilitating the establishment of different species than those dominating open habitats. Our findings have implications for the management of perennial shrubs and hydrological regimes in such wetlands.

Introduction

Recent decades have seen growing recognition of the significance of positive interspecific plant interactions (i.e. facilitation) to the diversity and dynamics of plant communities (Hacker & Gaines 1997; Michalet et al. 2006; Brooker et al. 2008; Butterfield 2009; Cavieres & Badano 2009; He et al. 2013). In particular, much research has focused

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on the role of 'nurse' plants in shaping understorey vegetation, especially in relatively harsh environments such as deserts, salt marshes and alpine areas (Li et al. 2010; Xu et al. 2010; Armas et al. 2011; Wang et al. 2011). Nurse plants, commonly dominant shrubs or tussock grasses facilitate the germination and growth of understorey herbs by ameliorating environmental stress at a microhabitat level so that the spatial and/or temporal ranges of less stress-tolerant species are extended, thereby enhancing local species richness (Niering et al. 1963; Flores & Jurado 2003). Mechanisms underlying such direct asymmetric facilitation can be either resource-based (e.g. provision of soil moisture or nutrients) or non-resource-based (e.g. alteration of temperature or protection from herbivory) or some combination of these (Bertness & Callaway 1994; Callaway 1995; Holmgren et al. 1997; Holzapfel & Mahall 1999; Bruno et al. 2003; Flores & Jurado 2003; Holzapfel et al. 2006). In arid environments, the establishment of understorey plants beneath shrub canopies may be further promoted by the influence of shrubs on propagule distribution, because shrub patches often retain higher proportions of seeds than bare interstitial areas (Reichman 1984; Aguiar & Sala 1997).

Nurse plants can also negatively affect understorey plants and therefore have the potential to reduce, as well as enhance, species richness. In arid environments, shrubs can negatively affect herbs by reducing light, intercepting scarce soil moisture (Tielborger & Kadmon 2000) and restricting seedling emergence through the accumulation of leaf litter (Barton 1993; Flores & Jurado 2003). Some studies also suggest that shrubs can promote their own encroachment of neighbouring vegetation communities by competitively reducing understorey herbs (Darrouzet-Nardi et al. 2008). Even when the direct effects of nurse plants on understorey plants are negative at the level of individuals or microhabitats, nurse plants may still increase species richness at a community level by supporting different assemblages of understorey species under their canopies than those of open areas (Cavieres & Badano 2009). A range of indirect facilitation mechanisms, whereby negative interactions between nurse plants and some understorey species result in less competitive exclusion amongst understorey plants overall, can contribute to the capacity of nurse plants to increase the local species pool (Levine 1999; Brooker et al. 2008; Soliveres et al. 2011).

The net overall effect of nurse plants on plant communities varies considerably in time and space, often in relation to changes in abiotic conditions, and much recent research has focused on understanding the outcomes of plant–plant interactions with respect to differences in environmental stress (Brooker et al. 2008). The 'stress-gradient hypothesis' (SGH), for example, predicts that positive interactions will be more common, intense or important with increasing levels of environmental stress, while competitive interactions should dominate under benign and productive conditions in which stress intolerant species are less reliant on nurse plants (Bertness & Callaway 1994; Lortie & Callaway 2006). At extreme levels of environmental stress, however, some studies suggest that facilitation effects may wane (Cavieres & Badano 2009; Holmgren & Scheffer 2010; Soliveres et al. 2011). There remains much to be resolved in our understanding of the relationship between plant–plant interactions and environmental gradients and further empirical studies to support conceptual developments are required (Brooker et al. 2008). Wetlands of arid and semi-arid environments provide a unique opportunity to study plant–plant interactions in hydrologically variable environments that alternate between extremes of highly productive conditions during flooding and relatively harsh conditions during periods of drought. In particular, shrub-dominated wetlands in such environments allow nurse plant effects to be studied in relation to this variability. The current study presents, to the best of our knowledge, the first investigation into nurse plant effects in such an environment.

We examine the effects of a widespread and dominant Australian shrub, *Duma florulenta* (Meisn.) T.M. Schust, previously *Muehlenbeckia florulenta* Meisn., commonly known as (tangled) lignum, on the composition and structure of understorey plant communities in a large semi-arid wetland in inland Australia: Narran Lakes. Such systems are characterized by high temporal and spatial variability in the presence and distribution of surface water, and hydrology is widely acknowledged as the principal driver of vegetation dynamics in these habitats (Capon 2003, 2005; Brock et al. 2006). During dry periods, understorey vegetation in these wetlands is often limited to very sparse cover of very few hardy species (e.g. Capon 2003). Many understorey plants in these environments maintain large, persistent soil seed banks and only appear in the extant vegetation during the favourable and highly productive conditions that follow floodwater recession (Capon & Brock 2006; James et al. 2007). Spatial variation in the composition and structure of extant vegetation communities, as well as soil seed banks, in these systems are typically governed by patterns of flood frequency and duration, with species richness and vegetation cover typically declining with decreasing flood intensity (Capon 2003, 2005; James et al. 2007). While much recent research has explored the influence of hydrology on germination, growth and reproduction in these plant communities (Capon 2003, 2005; Brock et al. 2006; Capon & Brock 2006; James et al. 2007), the role of plant–plant interactions in these environments is poorly understood.

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We sought to identify nurse plant effects, if any, of a dominant shrub (tangled lignum) on understorey herbs in a large semi-arid wetland, and to determine how these vary in mode (i.e. positive or negative) and contribution to understorey vegetation diversity both spatially, along a gradient of flood frequency and duration, and temporally, in relation to drying. We examined the net effect of lignum shrubs on understorey vegetation diversity along a spatial gradient extending from the most frequently flooded to the least frequently flooded parts of the shrublands' extent within the wetland. We also sampled vegetation on two occasions to compare the effects of lignum shrubs on understorey vegetation during highly productive conditions, following the recession of floodwaters, with harsher conditions occurring after 6 mo of drought. We explored potential mechanisms of facilitation by lignum shrubs by characterizing differences between shrub and open microhabitats, as well as by examining the distribution of the germinable soil seed bank.

Methods

Study area

The Narran Lakes is a large terminal wetland system situated in northern New South Wales in eastern Australia (29°43′ S, 147°26′ E). The region is hot, with maximum summer temperatures often exceeding 50 °C, and semi-arid, with a mean annual rainfall of 480 mm. Patterns of flooding in the wetland system are highly variable, both spatially and temporally, and are driven by flows in the Narran River, which is dry approximately 60% of the time. When flows do reach the wetland, a series of shallow lakes fill initially, given flows of sufficient magnitude and duration, followed by extensive areas of floodplain. Once full, the lakes may retain water for up to several years, while the intervening floodplains dry out over a period of months, depending on their position.

A significant proportion of the Narran Lakes wetland system is occupied by open shrubland dominated by *Duma florulenta* (Meisn.) T.M. Schust (hereafter lignum). Lignum is a large dioecious shrub in the Polygonaceae that occurs widely throughout floodplains of inland Australia, often comprising the dominant woody vegetation. This species tolerates both flooding and drying but varies in character in relation to flooding. In frequently flooded areas, lignum shrubland often comprises large dense clumps that may reach over 2.5-m tall, while sparse cover of small scattered plants (≦ 1-m tall) occurs in rarely inundated areas (Capon et al. 2009). Understorey vegetation in lignum shrubland usually comprises short grass and forb associations, often dominated by annuals that fluctuate in abundance and composition in response to flooding and drying. Large, diverse persistent soil seed banks are typically present (Capon 2003; James et al. 2007). Lignum shrubland provides valuable nesting habitat for colonial breeding waterbirds throughout inland Australia. With one of the largest extents of lignum shrubland remaining in eastern Australia, the Narran Lakes is a highly significant waterbird breeding site, especially for straw-necked ibis (*Threskiornis spinicollis*). In recognition of these values, around 5500 ha of wetland system were listed as a Ramsar site in 1999, and are also managed as a Nature Reserve by New South Wales National Parks and Wildlife Service.

Study design and data collection

We used flood extent maps, created from Landsat images of maximal annual flood extents between 1972 and 2004, to delineate three broad flood frequency zones within the extent of lignum shrubland in the Narran Lakes Nature Reserve. The high flood frequency zone was inundated by the maximum annual flood event in ca. 60% of years, while the low flood frequency zone included areas flooded in <10% of years. The medium flood frequency zone comprised areas of lignum shrubland between these two extremes.

Three replicate sites were randomly selected from each flood frequency zone for field surveys. At each site, a 50-m × 50-m plot was visually divided into shrub and open habitats. Shrub habitat was defined as the area directly beneath lignum shrub canopies, while open habitat comprised the remaining areas. In the high flood frequency zone, where lignum occurs in large dense thickets, areas in the centre of thickets that were typically occupied by impenetrable woody stems were excluded from the shrub habitat. Sampling was conducted within ten random quadrats (25 cm × 25 cm) in each habitat type per site. Open habitat quadrats were positioned at least 1 m away from the edge of the closest shrub's canopy.

Two vegetation surveys were conducted. The first, hereafter referred to as the 'wet' survey, followed the recession of a medium-sized flood event (42 000 ML recorded at Wilby Wilby gauging station, 43 km upstream of the reserve, in Nov 2004) that flooded ca. 8.65 km^2 of the nature reserve, inundating sites in the high flood frequency zone for ca. 6 mo, and those in the medium flood frequency zone for up to 3 mo. Sites in the low flood frequency zone were not inundated during this event, but conditions were still relatively wet at this time due to higher than average rainfall in preceding months. A second 'dry' survey was undertaken following a 6-mo period of drought (May 2005). At this time, only a small amount of surface water remained in the wetland system in one of the deeper, northern lakes (Clear Lake) but not in any of the wetland area occupied by lignum shrubland.

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During each survey, all understorey species in each quadrat were recorded and their abundance estimated as percentage cover. For each quadrat, we also estimated percentage canopy cover (including lignum canopy) using a spherical densitometer on both surveys, and percentage leaf litter cover during the second survey. Aggregate soil samples, comprising three 5-cm deep cores, were collected from the centre of each quadrat during the first survey to determine soil characteristics and soil seed bank composition. Previous studies in comparable systems have found little variation in soil seed bank composition over such time periods, even in response to large flood-induced germination events (Capon & Brock 2006).

We examined the germinable soil seed bank via a seedling emergence experiment conducted at the Northern Basin Laboratory of the Murray-Darling Freshwater Research Centre at Goondiwindi, ca. 300 km northeast of Narran Lakes. Soil from each quadrat was placed in a single plastic tray (dimensions 6.3 cm × 11 cm) to a depth of 2.5 cm, moistened and positioned randomly in one of three clear plastic covered frames under ambient light and temperature conditions. Trays were watered approximately three times a week for 20 wk during the Austral summer and autumn. All seedlings emerging during the experiment were harvested upon flowering, before contributing to the seed bank themselves, and identified. Pooled subsamples of soils collected from each habitat type in each site were used to determine soil organic matter, particle size, pH, phosphorus and nitrogen. Soil organic matter was measured by combustion, and particle size via a Malvern 2000 laser particle size analyser. Phosphorus concentration was analysed using a Varian Vista AX simultaneous axially viewed Inductively Coupled Plasma Atomic Emission Spectrometer (Varian Systems, Palo Alto, Ca, US), and nitrogen with a C-N nutrient analyser.

Data analysis

We calculated total abundance (i.e. summed percentage cover) and species density (i.e. number of species) for each field survey quadrat and experimental tray. We also calculated the species richness of the understorey plant community and germinable soil seed bank for each habitat type at each site by summing all species present across all quadrats (or trays). Both data sets were analysed using a split-plot ANOVA model with flood frequency (low, medium or high) and habitat (shrub or open) as fixed factors and site (three levels) nested within flood frequency as a random factor. Field survey data for each season were analysed separately due to significant interactions between season and other terms in initial analyses. All data were transformed (log+1 or square root) prior to analyses to improve data normality and homogenize variance. Significantly different means were explored via Tukey's tests.

Effects of flood frequency and habitat type on understorey vegetation and soil seed bank composition were explored using permutation multivariate analyses based on Bray-Curtis dissimilarities of log+1 transformed abundance data (PERMANOVA; Anderson 2005). The significance of each term was tested using 4999 permutations. Where the number of unique permutations was low, however, *P*-values are derived by a Monte Carlo random sample from the asymptotic permutation distribution (Anderson & Robinson 2003). Permutation tests of multivariate dispersion were made using PERMDISP (Anderson et al. 2006). The SIMPER procedure in PRIMER (Clarke 1993) was used to examine the percentage contribution of each species to the similarity within flood frequency/habitat groups and dissimilarity between flood frequency/habitat groups. Multivariate analyses could not be performed using data from the second field survey due to the high number of empty cells.

Results

Canopy cover and soil characteristics differed between shrub and open habitats in all flood frequency zones (Fig. 1, Appendix S1). As there were few trees present in study sites, canopy cover was substantially higher under shrubs (ca. >80%) than in open habitats (ca. <1%) but did not differ at a quadrat level between flood frequency zones or survey times (Fig. 1). Visible reductions in the stature and density of lignum shrubs were apparent, however, with declining flood frequency. High flood frequency zones were occupied by distinct islands of tall (>2.5 m) mature shrubs, intersected by clear flood-runners. In contrast, medium and low flood frequency sites supported smaller individuals with a less clumped distribution.

Litter cover was higher in shrub habitats than in open habitats and also tended to increase with flood frequency (flood frequency × habitat: $P \leq 0.001$; Fig. 1a, Appendix S1). Soil organic matter increased with increasing flood frequency (flood frequency: $P \leq 0.05$; Fig. 1b, Appendix S1) and tended to be higher under shrubs than open habitats, although this effect was not significant. Soil pH was generally lower under shrubs, particularly in the low flood frequency zone where soils were less alkaline overall (flood frequency × habitat: $P \leq 0.05$; Fig. 1c, Appendix S1). Sand content of soils, typically lowest in the high flood frequency zone, was higher under shrubs across all flood frequency zones (habitat: $P \leq 0.05$; Appendix S1), but neither silt nor clay levels differed between shrub and open habitats (Fig. 1d–f, Appendix S1). Total soil nitrogen was substantially higher under shrubs in the frequently flooded zone but not elsewhere (flood frequency × habitat:

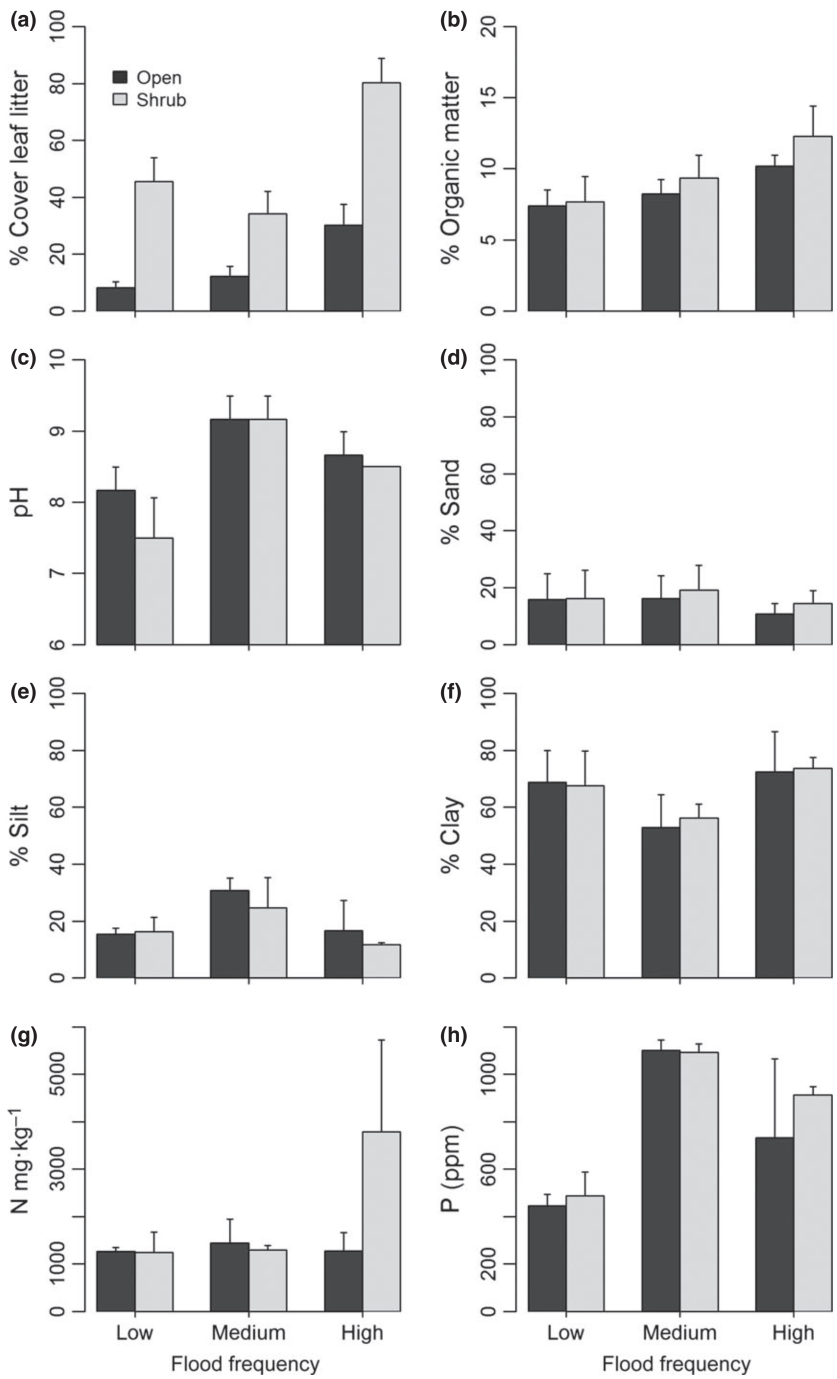

Fig. 1. Soil characteristics of open and shrub habitats in each flood frequency zone: (**a**) percentage cover of leaf litter, (**b**) percentage organic matter, (**c**) pH, (**d**) percentage sand, (**e**) percentage silt, (**f**) percentage clay, (**g**) nitrogen and (**h**) phosphorus. Mean values are shown and error bars indicate SE.

$P \leq 0.05$; Fig. 1g, Appendix S1). A similar, though not significant, trend was evident for phosphorus (Fig. 1h, Appendix S1).

Over 61 species, mostly annual forbs and sedges, were observed in the understorey during the wet survey (Appendix S2). Fourteen species, including the twining forbs *Einadia nutans* subsp. *nutans* and *Stellaria angustifolia*, were only observed under shrubs at this time. The majority of species restricted to shrub habitats were rare, typically with only a few individuals occurring in one (nine species) or two (two species) quadrats. In contrast, the eight species present only in open habitats during the wet survey mostly occurred in moderate abundance and frequency. During the dry survey, only 13 understorey species were recorded, all of which were present during the wet survey, except for two chenopod sub-shrubs, *Sclerolaena muricata* and *Maireana triptera* (Appendix S2). Six species occurred solely under shrubs at this time and two were recorded only in open habitats. At both survey times, a larger proportion of species were restricted to shrub habitats within the low and high flood frequency zones. The proportion of species only occurring in open habitats was higher at both times in the low flood frequency zone.

Species richness, density and total cover declined substantially between the two survey times and spatially with decreasing flood frequency during the wet survey, but not the dry (Fig. 2, Appendix S3). Species richness (i.e. at the site scale) was higher in shrub habitat than open habitat in the high and medium flood frequency zones during the wet survey (flood frequency × habitat: $P \leq 0.01$; Fig. 2a, Appendix S3), and in all flood frequency zones during the dry survey (habitat: $P \leq 0.01$; Fig. 2b, Appendix S3). Species density (i.e. at the quadrat scale) during the wet survey was only higher under shrubs in the high flood frequency zone (although habitat was not a significant overall effect; Fig. 2c, Appendix S3), but was significantly higher under shrubs in all flood frequency zones during the dry survey (habitat: $P \leq 0.01$; Fig. 2d, Appendix S3). Differences in species richness and density were particularly pronounced in the high flood frequency zone for both survey times (Fig. 2). In all flood frequency zones, total understorey cover was lower under shrubs than in open habitats during the wet survey (habitat: $P \leq 0.01$; Fig. 2e, Appendix S3) and higher during the dry survey (habitat: $P \leq 0.01$; Fig. 2f, Appendix S3).

The composition of understorey vegetation was very heterogeneous at a site level during the wet survey, varying in relation to both flood frequency and habitat and their interaction (flood frequency × habitat; $P = 0.01$; Appendix S4). A significant effect of habitat type on composition was only approached (although not significant) in the high flood frequency zone (Appendix S5). Species contributing to the dissimilarity between shrub and open habitats in the high flood frequency zone included *Cullen cinereum* (contributing to 9.2% of the dissimilarity), *Polygonum plebeium* (8.8%), *Cyperus pygmaeus* (7.8%) and *Centipeda cunninghamii* (5.7%), all of which were more abundant in open habitats, and *Trigonella suavissima* (6.4%), *Calotis scapigera* (6.3%) and *Rumex crystallinus* (6.1%), which were more abundant under shrubs.

At least 45 species, predominantly annual forbs and sedges, were present in the germinable soil seed bank. Neither flood frequency nor habitat type had a significant influence on the abundance, species richness or species density of seedlings germinating from the soil seed bank (Fig. 3, Appendix S6). The overall composition of germinable soil seed banks, however, did vary in relation to both flood frequency and habitat independently of each other (no significant flood frequency by habitat interaction; Appendix S4). Differences in seed bank composition were apparent for all flood frequency pair-wise combinations, but habitat differences were only apparent in the high flood frequency zone (Appendix S5). Species contributing to this habitat dissimilarity included *Cyperus pygmaeus* (contributing to 19.6% of the dissimilarity) and *Polygonum plebeium* (14.1%), both more abundant from open habitat, and *Centipeda cunninghamii* (18.1%), which germinated more frequently from shrub habitat. All of these species were abundant in the extant vegetation of the high flood frequency zone during the wet survey, where *Cyperus pygmaeus* was similarly restricted to open habitats, while the other two species occurred in both habitats.

Discussion

Interspecific plant interactions are integral to vegetation dynamics and the composition and structure of all plant communities reflect, to some extent, the net outcome of multiple, simultaneous positive and negative interactions (Holmgren et al. 1997; Bruno et al. 2003; Brooker et al. 2008). In the large semi-arid wetland system of the Narran Lakes, we found that lignum shrubs exert an array of positive and negative influences on understorey plants across a range of scales, and that the net effects of these nurse plant interactions on understorey vegetation vary over time, in relation to drying, and in space, with respect to flood history. Overall, lignum shrubs appear to make a significant contribution to community diversity in this semi-arid wetland by enhancing the local species pool of understorey plants through both direct (e.g. microhabitat amelioration) and indirect facilitative pathways.

Classic positive nurse plant effects of lignum shrubs on understorey plants were clearly apparent during both wet and dry survey times. This was particularly the case during the dry survey when species richness, density and understorey plant cover were all consistently higher under shrubs than in open areas across the entire floodplain gradient. Other studies (e.g. Armas et al. 2011) have similarly found that a significant portion of understorey species that may thrive under mesic conditions can only survive under nurse plants under conditions of high aridity. Facilitation mechanisms involved under these dry conditions may include the provision of soil moisture, since vegetation is strongly limited by water availability in semi-arid and arid floodplain wetlands during periods intervening floods (Capon 2003; Brock et al. 2006). Although we can only speculate on the facilitation mechanisms at play here, shrub microhabitats tended to have higher levels of soil

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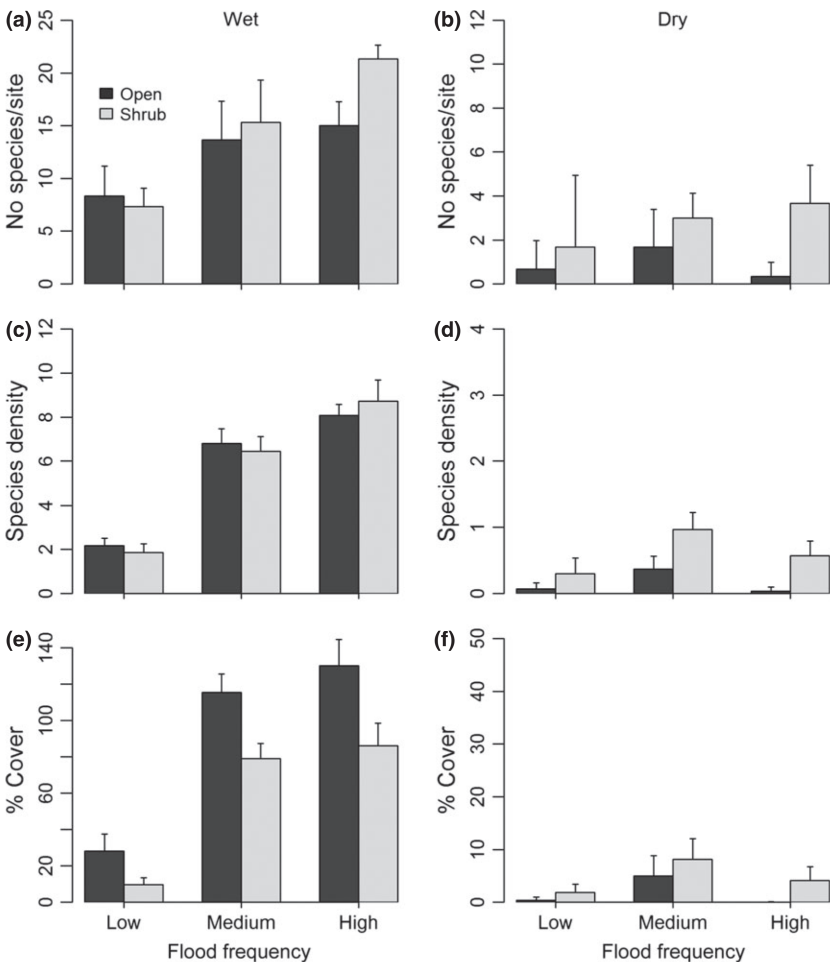

Fig. 2. (**a**, **b**) Species richness (**c**, **d**) species density and (**e**, **f**) total cover of understorey plant communities in open and shrub habitats in each flood frequency zone during wet and dry surveys. Mean values are shown and error bars indicate SE. N.B. Since total cover represents the summed cover of all species occurring within a quadrat, cover values may exceed 100%.

organic matter than open areas, and other studies have found this often correlates positively with soil moisture under shrubs in semi-arid environments (Joffre & Rambal 1993; Pugnaire et al. 2004). Microhabitat amelioration through shading (e.g. lowering of temperature) and protection from herbivory may also contribute to the facilitative effects observed under dry conditions. The high proportion of understorey species restricted to shrub habitat at this time suggests that direct facilitation by lignum shrubs allows many species to persist longer into drought periods than they might otherwise in the absence of shrubs. Consequently, positive nurse plant interactions appear to be a key driver of understorey vegetation diversity in this semi-arid wetland during dry phases.

Positive effects of lignum shrubs on understorey vegetation were also apparent during the wet survey, predominantly in the highest frequently flooded zone, where shrubs increased both species richness and species density and, to a lesser degree, in the medium flood frequency zone, where only species richness was higher in shrub habitat. In contrast to the low flood frequency zone, both of these zones had been inundated prior to the wet survey. The slightly elevated microhabitats that occur under lignum shrubs may alleviate abiotic stresses associated with soil waterlogging following flooding for some species (e.g. soil anoxia), as occurs under tussock grasses in some salt marshes (Wang et al. 2011). The larger and more established shrubs of the highest frequently flooded zone might therefore be able to support a larger range of species than smaller shrubs in the medium flood frequency zone where microhabitat elevation is probably less distinct between shrubs and open patches. Previous studies have also observed an influence of nurse plant size on their facilitative effects in arid environments (Tewksbury & Lloyd 2001; le Roux et al. 2013).

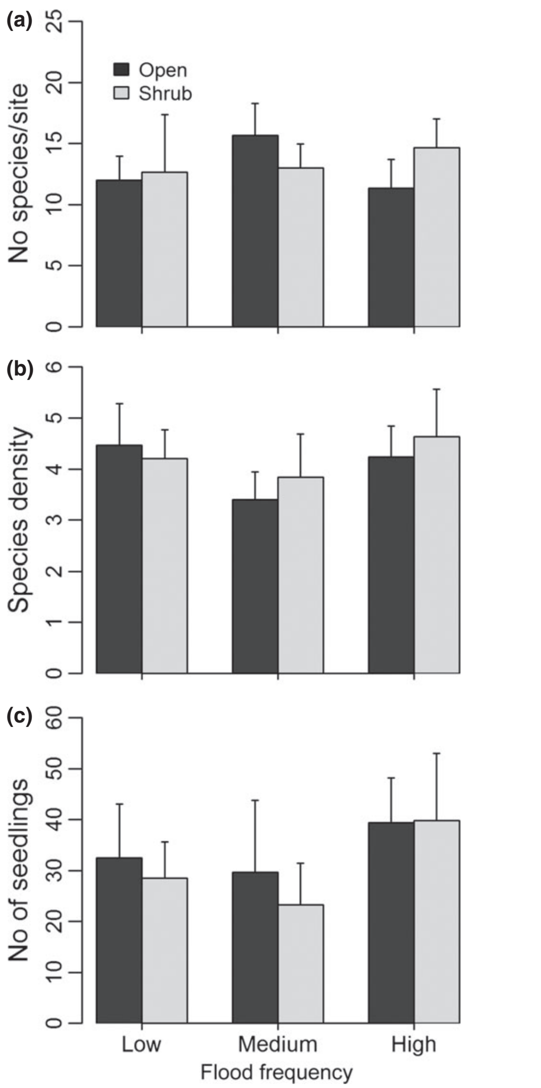

Fig. 3. (**a**) Species richness, (**b**) species density and (**c**) total abundance of the germinable soil seed bank from open and shrub habitats in each flood frequency zone. Mean values are shown and error bars indicate standard error.

Our results also demonstrate that lignum shrubs contribute positively to increased understorey plant diversity by providing support for twining species (e.g. *Einadia nutans* subsp. *nutans* and *Stellaria angustifolia*). Such facilitative effects were apparent under both wet and dry conditions. Facilitation mechanisms involving the influence of nurse plants on propagule distribution, however, do not appear to be significant in this wetland, since lignum shrubs were found to have limited effects on spatial patterns in the germinable soil seed bank. Differences detected in soil seed bank composition between shrub and open habitats in the frequently flooded zone probably reflect extant vegetation and recent seed additions rather than a longer-term influence of shrubs on propagule dispersal and accumulation.

We also found clear evidence that lignum shrubs exert a substantial negative influence on some understorey plants, particularly under the productive and relatively favourable conditions that follow floodwater recession. During the wet survey, shrubs reduced understorey vegetation cover across the entire flood frequency gradient, as well as species density in the low and medium flood frequency zones. These competitive interactions may be due to shading and possibly inhibiting effects of high leaf litter cover under shrubs on germination (Barton 1993; Flores & Jurado 2003). Negative effects of lignum shrubs were particularly evident amongst the more abundant understorey species present, since these contributed most to differences between shrub and open assemblages and were also more likely to be restricted to open habitats, both within flood frequency zones and overall. Despite the negative effects of lignum shrubs on understorey vegetation observed at this time, however, our results indicate that positive nurse plant interactions make a significant contribution to vegetation diversity under wet conditions at a community level by adding rare species to the species pool (Cavieres & Badano 2009). Rarer species present during the wet survey were more likely to only occur under shrubs in contrast to abundant species, which tended to be more common in, or restricted to, open habitats. This suggests that lignum shrubs may facilitate the germination and growth of less competitive understorey species through the suppression of competitive dominants (i.e. indirect facilitation; Levine 1999).

We did not detect any waning of facilitative effects in relation to drying, as has been observed below certain thresholds of water availability amongst nurse plants and their beneficiaries in other arid habitats (Bertness & Callaway 1994; Holmgren et al. 1997; Armas & Pugnaire 2005). Even under the driest conditions examined (i.e. in the low flood frequency zone during dry conditions), shrubs had strong positive effects on species density, total cover and species richness. It is improbable that lignum shrubs would ever compete for soil moisture resources with most of the relatively stress-tolerant understorey herbs present during dry periods in the Narran Lakes, since lignum roots grow deeply and rapidly (Capon et al. 2009) and therefore may access different soil moisture reserves than those available to understorey herbs with roots that are mostly confined to upper soil layers.

Conclusions

In lignum shrubland of the Narran Lakes we found that nurse plant interactions contribute to the diversity of understorey plant communities, and these vary in their mode

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and net effects both spatially and temporally. Under dry conditions, we found that lignum shrubs have a predominantly positive effect on understorey plants. Under favourable and productive conditions following floodwater recession, lignum shrubs exert negative influences on the more abundant and dominant understorey species, but appear to facilitate the establishment of rarer species, increasing species diversity at a site scale. Our findings have implications for management of perennial shrubs in these wetlands, particularly with regard to the management of flooding regimes.

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Supporting Information

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

Appendix S1. Results of ANOVA for main effects and interactions on soil characteristics.

Appendix S2. Understorey plant species present in shrub and open habitats in each flood frequency zone during wet and dry field surveys.

Appendix S3. Results of ANOVA under wet and dry field surveys for main effects and interactions on understorey vegetation metrics.

Appendix S4. Results of PERMANOVA on the composition of understorey vegetation during the wet field survey and seedlings germinating from the soil seed bank.

Appendix S5. *t*-values and significance levels from pair-wise comparisons conducted after PERMANOVA of the composition of understorey vegetation during the wet field survey and seedlings germinating from the soil seed bank.

Appendix S6. Results of ANOVA for main effects and interactions on the number of species and seedlings germinating from the soil seed bank.

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