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Spatial variability of the soil seed bank in a heterogeneous ephemeral wetland system in semi-arid Australia

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Abstract

Soil seed banks are an important component of plant community diversity in ephemeral wetlands, allowing many species to persist through unpredictable periods of flood and drought. Spatial variation of extant vegetation in such habitats commonly reflects patterns of flood history and often varies predictably between broadly differing hydro-geomorphic habitat types. Here we investigate whether spatial variation of soil seed banks is similarly controlled by fluvial processes at this scale. Results are presented from a seedling emergence trial using samples collected from a range of habitat types, and at different scales within these, in the ephemeral Narran Lakes system in semi-arid Australia. Composition and structure of soil seed banks varied significantly between habitat types reflecting broad differences in flood frequency. As predicted, germinable seed abundance was found to be highest in intermediately flooded habitats. Variability in soil seed bank composition at a local scale was also found to be influenced by hydrology with greater spatial heterogeneity evident in the river channel as well as amongst the least frequently inundated riparian and floodplain habitats.

Keywords

Riparian vegetation; flooding; hydrology; vegetation dynamics; germination

Introduction

Persistent soil seed banks comprise an important component of plant community diversity in ephemeral wetlands (Bonis *et al.* 1995; Brock & Rogers 1998; Brock *et al.* 2003). By definition, such environments are highly temporally variable as conditions fluctuate, often unpredictably, between flooding and drying.

Consequently, soil seed banks enable many annual and some perennial plant species to persist in a dormant state through unfavourable periods of drought and become re-established during or following inundation. As germination cues (e.g. flooding, light or temperature) as well as growth responses to flooding and drying vary amongst species residing in the soil seed bank (Baskin & Baskin 1998), extant plant communities in ephemeral wetlands are often highly dynamic, exhibiting significant shifts in composition over time in response to hydrological conditions (Haukos & Smith 1993; Bonis *et al.* 1995; Casanova & Brock 2000; Capon 2003; Nicol *et al.* 2003).

Ephemeral wetlands associated with riverine systems also exhibit high spatial heterogeneity as a result of complex interactions between fluvial dynamics, geomorphologic landform and position (Hupp & Osterkamp 1996; Stromberg 2001). Such wetland systems can be perceived as dynamic mosaics of hydro-geomorphic habitats within which soil moisture, nutrient and sediment characteristics vary. Wetland plant community distributions tend to reflect these localised conditions since species differ in their responses to flooding and drying (Blom & Voesnek 1996). Consequently, hydrology is generally regarded as the primary determinant of spatial patterns in vegetation composition and structure in ephemeral wetlands with geomorphology playing an important secondary role in those systems situated in fluvial settings (Haukos & Smith 1994; Hupp & Osterkamp 1996; Higgins *et al.* 1997; Capon 2003; Capon 2005).

Wetland soil seed banks often differ substantially in composition from their corresponding extant plant communities at any particular time and may resemble a range of phases (van der Valk and Davis 1978) or a specific phase of vegetation which occurs in response to certain hydrological conditions, e.g. drawdown (Leck 1989). In more extreme cases, wetland soil seed banks are dominated by species which are absent from the extant vegetation (Thompson & Grime 1979; McGraw 1987; Hughes & Cass 1997). Nevertheless, it could be expected that broad spatial patterns in soil seed bank composition and structure in many wetlands might still be explained at the hydro-geomorphic habitat scale. The composition of persistent soil seed banks reflects past vegetation changes (LaDeau & Ellsion 1999; Rossell & Wells 1999; Wetzel *et al.* 2001) as well as processes which influence their depletion (e.g. germination, mortality, granivory and scouring) and replenishment (e.g. dispersal). As hydrology and geomorphology often have an overriding influence on such factors in floodplain wetlands (Junk *et al.* 1989; Walker *et al.* 1995; Stromberg 2001), soil seed bank composition should therefore vary with some degree of predictability between habitat types.

Whilst soil seed banks of tidal marshes often exhibit strong spatial patterns with respect to hydrological variation (Parker & Leck 1985), previous studies of ephemeral wetlands have, however, found little differentiation in soil seed bank composition along spatial gradients of flood frequency, water depth or elevation. At the within-wetland scale, for example, soil seed bank density and composition were found to be relatively homogeneous along elevational gradients in ephemeral playa wetlands of the southern United States (Haukos & Smith 1994) and in temporary Mediterranean marshes, seed composition and density exhibited only slight variation with water depth (Bonis *et al.* 1995). Similarly, common species were widely distributed throughout the soil seed bank of a large ephemeral floodplain in arid central Australia, although a significantly higher abundance of germinable seeds was recorded in more frequently flooded areas (Capon & Brock 2006). At a larger scale, studies comparing temporary wetlands with varying flood histories have also found little influence of hydrology on the abundance or composition of soil seed banks (Brock 1998; Brock & Rogers 1998). To the best of our knowledge, however, effects of geomorphological habitat differences on soil seed bank composition and structure in heterogeneous fluvial ephemeral wetland systems in semi-arid areas have not been investigated.

In most cases, soil seed banks of ephemeral wetlands, as in other systems, are extremely patchy at a local or microtopographical scale (Brock *et al.* 1994; Bonis *et al.* 1995). It is possible that this local variability in soil seed bank composition itself may depend on hydro-geomorphic processes (Capon & Brock 2006). Within rarely flooded habitats, for example, greater spatial variation is likely as factors other than flooding (e.g. mortality, granivory and secondary dispersal by wind) could have more influence on the distribution of propagules within the soil seed bank. Similarly, soil seed bank composition might be expected to be less variable within hydro-geomorphic habitats which receive frequent inundation as propagules will be dispersed more homogenously by floating on floodwaters (Haukos & Smith 1994; Bonis *et al.* 1995). Such relationships between local spatial variability in soil seed bank composition and fluvial processes may have been overlooked in previous studies of ephemeral wetlands which have examined patterns at a single scale.

Here, we hypothesise that broad spatial patterns in the soil seed bank structure will be explained at the hydro-geomorphic habitat scale. We present the results of a study of spatial variation in the soil seed bank of a heterogeneous ephemeral floodplain wetland system in semi-arid Australia; the Narran Lakes. We examine the diversity, abundance and composition of the germinable soil seed bank at several different scales between and within major hydro-geomorphic habitat types. The principal aims of this study were to identify the occurrence of any spatial patterns in soil seed bank composition and structure with relation to hydro-geomorphic habitat and secondly, to establish the scale (i.e. between habitats, between sites within habitats or within sites) at which soil seed bank variability occurs and determine whether or not this is likely to be influenced by hydrology.

Methods

Study area

The Narran Lakes is an ephemeral floodplain wetland system located in the semi-arid north-west of New South Wales, Australia. It is an allogenic system dependent upon flows in the Narran River, a distributary of the Condamine-Balonne river system which straddles the New South Wales and Queensland border (Fig. 1). According to the Köppen Climate Classification system the Narran Lakes region is hot, persistently dry grassland (Stern *et al.* 2000). Maximum summer temperatures often exceed 50 °C while winter minimums are around 20 °C (Fig. 2). The long term (1920-2000) average annual rainfall at Walgett, about 75 km from the Narran Lakes, is approximately 480 mm a year but annual rainfall can range from 266 mm to 690 mm. Rainfall is highly variable both within and between years with a pronounced wet/dry periodicity (Fig. 2), a common feature of semi-arid and arid regions of Australia (Gentilli 1986). Mean annual evaporation rates of about 2 m substantially exceed the annual rainfall receipt indicating a large negative water balance in the Narran Lakes area.

The local catchment area of the Narran Lakes wetland system is quite small (~50 km^2). Consequently, the lakes do not fill as a result of local precipitation. Rather, floods in the Narran River, which are usually generated in the upper reaches of the Condamine-Balonne river basin, are responsible for lake-filling events. The Narran River is dry approximately 60 % of the time but, during flood years, flows may reach greater than 8 000 ML/day. The high inter-annual variability of flows in the Narran River (Fig. 3) insures that the Narran Lakes has a complex flood history with periodic wet/dry cycles.

The Narran Lakes wetland system comprises several relatively distinct water bodies including Clear Lake, Back Lake and Long Arm in the north and Narran Lake in the south as well as large areas of floodplain throughout (Fig. 1). When flood waters enter the system, Clear Lake fills first, then Back Lake, Long Arm, and, if the event is sufficiently large, Narran Lake. Percentage of times inundated and the duration of inundation following a single flood event of identified major hydro-geomorphic habitats during a 23 year period were determined from satellite imagery analysis (Table 1).

A significant portion (5 500 ha) of the northern section of the Narran Lakes were designated as a Ramsar site in June, 1999. This area has also been managed as a Nature Reserve by New South Wales National Parks and Wildlife Service since 1988. The wetland system is characterized by large areas of the flood-tolerant shrub *Muehlenbeckia florulenta* Meisn. (tangled lignum) which provides an important breeding habitat for waterbirds, most notably *Threskiornis spinicollis* (straw-necked ibis). Land use in the surrounding region is predominantly sheep grazing and mineral exploration. Further upstream, in the northern part of the Condamine-Balonne, land use is increasingly dominated by intensive crop irrigation which has been associated with substantial water resource developments in recent years, influencing the catchment's hydrology on a number of scales (Thoms & Sheldon 2002). Consequently, altered hydrology is currently perceived as a major threat to the ecological integrity of the Narran Lakes Ramsar site (Thoms & Parsons 2003).

Experimental design

Three sites were selected randomly from each predefined hydro-geomorphic habitat (Table 1). Within each site, three replicate sediment samples were collected from locations approximately 100 m apart. Each replicate sample comprised 10 aggregated random surface sediment cores of 5 cm depth and a diameter of 10 cm collected from within a 10 m^2 quadrat. All sediments were collected in December 2003 and January 2004 following a 2 year period of drought in the wetland. Extant vegetation was not assessed at the time of soil collection as the sites were largely devoid of vegetation. Following collection, samples were returned to the laboratory, sorted to remove large debris, mixed and stored until the commencement of the experiment.

Experimental procedure

A seedling emergence experiment was conducted outside at the Northern Basin Laboratory of the Murray-Darling Freshwater Research Centre, Goondiwindi, Queensland, approximately 300 km to the north east of the Narran Lakes system. Sediment from each replicate sample was used to fill two plastic trays (with dimensions of 16.3 cm x 11 cm) to a depth of 2.5 cm. This resulted in a total of 126 containers reflecting 7 habitats x 3 sites nested within habitats x 3 replicate samples within sites x 2 trays. Trays from each sample were then subjected to one of two watering treatments; a waterlogged treatment in which soil was kept wet for the duration of the experiment and a submerged treatment in which trays were placed within individual 4 L plastic boxes and flooded to a depth of 10 cm. Previous studies of seed banks from this area indicate that water depth does not significantly influence the composition or abundance of germinating seedlings (Casanova & Brock 2000).

All experimental trays were randomly placed in two large wire frames covered with thick clear plastic to prevent disturbance by rainfall and were re-randomised every three weeks. In order to expose samples to a range of temperatures, the experiment was run for a period of 5 months from late summer to the middle of spring in 2004. During this period air temperatures ranged from a maximum of approximately 30°C to a minimum of 18°C in March to a maximum of 21°C and a minimum of 5.6°C in August. Plant species germinating in trays were harvested upon flowering and prior to any further contribution of seeds to the sediment. Voucher specimens of each species were photographed, pressed and verified by comparison to herbarium samples at the herbarium of New South Wales in Sydney. At the termination of the experiment, remaining species were transplanted and grown in pots until identification was possible. Additional trays containing vermiculite were also monitored throughout the experiment in order to detect the presence of seeds that might have dispersed by wind into experimental trays. As no seedlings emerged in these during the experiment, it was assumed that all germinating seedlings originated from the soil seed bank of the collected sediment samples.

Statistical analyses

Total seedling abundance, species richness and Berger-Parker dominance, calculated as the seedling abundance of dominant species divided by total seedling abundance (Southwood & Henderson 2000), were calculated for each tray. Total seedling abundances were square root transformed to homogenize variances. In order to detect significant differences in each of these variables between hydro-geomorphic habitats and sites, data were then analysed using a partially nested mixed model analysis of variance. In these analyses, hydro-geomorphic habitats were treated as fixed variables and sites nested within habitats and replicates within sites as random variables. All univariate analyses were conducted in S Plus (Insightful Corp., Seattle, WA, U.S.A.).

Multivariate analyses were also performed in order to examine patterns in the composition of germinating seedlings. Under the submerged treatment vegetation responses were scant, with some samples totally devoid of germinating seedlings. Multivariate analyses, therefore, were only performed on the waterlogged treatment data. Initially, species abundance data for each tray was square root transformed and a matrix of dissimilarities between each pair of replicates was calculated using the Bray-Curtis dissimilarity coefficient. To examine patterns of assemblages amongst habitats a two-way nested analysis of similarities (ANOSIM) was performed using Primer version 5.2.9 (Carr 1996). This is a non-parametric test used to investigate the average of rank similarities between predefined groups. ANOSIM generates an R test statistic which is scaled between -1 and +1. A pair-wise comparison between R values then examines how distant groups are from each other. A zero value represents the null hypothesis of no difference implying similarities between and within groups are about the same. Values of 1 indicate all replicates within groups are more similar to each other than replicates from different groups.

Further investigation of compositional differences in the soil seed bank was achieved using Non-Metric Multidimensional Scaling (nMDS). Both the complete dataset of species abundances and a modified dataset with rare species (those occurring in ≤ 1% of samples) removed were examined. As these datasets produced similar results, the full dataset was used for all subsequent analyses. This analysis was performed in three dimensions using rank orders of similarity. Species vectors significantly correlating with the ordination space were also calculated using the principal axis rotation (PCR), principal axis correlation (PCC) and Monte-Carlo Randomisation (MCAO) procedures in the PATN software package (Belbin 1995).

Results

A large and diverse germinable soil seed bank was found to be present. A total of 77 species germinated from the sediment samples during the experiment, comprising 23 monocot and 54 dicot species representing 33 families. Common species included the sedge *Cyperus pygmaeus* Rottb. (Cyperaceae) and the forbs *Centipeda cunninghamii* A.Braun & Asch. (Asteraceae), *Ammania multiflora* Roxb. (Lythraceae) and *Polygonum plebeium* R.Br. (Polygonaceae). Considerably fewer species germinated under submerged conditions (11 species) than waterlogged (76 species) and of these only one, the charophyte *Nitella* sp., was restricted to submerged samples. Furthermore, seedlings germinating under submerged conditions only accounted for 5.7 % of the total number which germinated during the experiment.

Seedling abundance ranged from 0 to 227 seedlings per tray with the greatest numbers occurring in samples from the intermediately flooded habitats, i.e. Back Lake centre, Clear Lake shore and the lignum floodplain (Fig. 4a). Mean seedling abundance was found to be significantly different between habitats although a significant interaction with treatment was found (Table 2), possibly as a result of the low abundance of seedlings emerging under submerged conditions from the Narran River channel samples (Fig. 4a). Significant differences in seedling abundance were also detected between sites within habitats but not between replicates within sites (Table 2).

The species richness of germinating seedlings ranged between 0 and 23 species per tray and was greatest in samples from the two floodplain habitats (Fig. 4b). The lowest mean species richness occurred in samples from the most frequently flooded habitats, i.e. Clear Lake centre and Narran River channel. Mean species richness was also found to differ significantly between habitats but a significant interaction with treatment was again detected (Table 2). Visual inspection of the data indicated that this may be a result of the relatively low number of species germinating under submerged conditions in samples from the chenopod floodplain in comparison with their overall high species richness (Fig. 4b). Sites within habitats, but not replicates within sites, were also found to differ significantly from each other (Table 2).

Dominance, as indicated by Berger-Parker indices, did not differ significantly between habitats, treatments or sites within habitats (Table 2), although submerged treatments exhibited greater dominance than waterlogged ones in all habitats but the most and least frequently flooded (Fig. 5a). Samples from the chenopod floodplain also tended to have the lowest dominance. Amongst the waterlogged samples, the two most frequently flooded habitats, also those with the lowest mean species richness, had the highest mean dominance (Fig. 5a). Species which were unique to a particular habitat were recorded in every habitat type except for the two with the highest seedling abundance, Back Lake centre and Clear Lake shore, although these did have species which occurred in samples from only two (rather than one) habitats (Fig. 5b). Furthermore, the highest numbers of species unique to a particular habitat germinated in samples from the two floodplain habitats which were also the habitats with the greatest species richness (Fig. 5b).

The composition of germinating seedlings differed significantly between most habitats with three relatively discrete groups apparent in the ordination (Fig. 6, Table 3). Of these, the two least frequently flooded habitats, the chenopod floodplain and the river bank, exhibited the most differentiation in comparison to other habitat types and each other, with the majority of replicates from each occupying their own distinct regions in the ordination space (Fig. 6a). Species related to this separation included a mixture of forbs, grasses and sedges (Fig. 6b, Table 4). Samples taken from the remaining habitats, particularly Back Lake centre, Clear Lake centre and Clear Lake shore, appeared to be more closely aligned with each other in terms of composition (Fig. 6a) but replicates were still significantly more similar to each other within these groups than between groups (Table 3). In contrast to the chenopod floodplain and river bank, the species vectors correlating significantly with the position of these samples in the upper left quadrant of the ordination space were almost exclusively dicotyledonous with the exception of a single sedge species (Fig. 6b). The greatest overlap in composition occurred amongst samples from the two most frequently flooded habitats, the river channel and Clear Lake centre (Table 3). Samples from the lignum floodplain also displayed considerable overlap in composition with the other two habitats dominated by lignum shrubland, Clear Lake shore and Back Lake centre (Table 3).

The degree of variability in composition between replicates within sites and sites within habitats, as indicated by pair-wise comparisons of Bray-Curtis dissimilarity scores, also differed between habitat types (Fig. 7). At both scales, composition tended to be the least variable in the three lake habitats; Back Lake centre, Clear Lake centre and Clear Lake shore, while samples from the least frequently flooded habitat, the chenopod floodplain, exhibited the greatest variability (Fig. 7). Samples from the most frequently flooded habitat, the Narran River channel, were also relatively dissimilar from each other, particularly at the site level (Fig. 7).

Discussion

Soil seed bank composition and structure at any time and place necessarily represents the results of recent historical transactions of propagule replenishment and depletion from the sediment. We hypothesise that, in dryland ephemeral wetlands associated with riverine systems, such transactions are likely to be strongly influenced by fluvial processes and that soil seed banks should, therefore, exhibit spatial patterns which are closely related to hydro-geomorphic habitat types. In a particular habitat, for instance, the soil seed bank should contain a significant proportion of propagules derived from phases of the extant vegetation which have occurred locally in response to that habitat's distinctive hydrologic characteristics. Soil seed bank composition should therefore reflect the morphological, physiological and life history traits that enable species to tolerate or avoid the constraints imposed by that local water regime.

The quantity of locally derived seeds entering soil seed banks may also vary between dryland ephemeral wetland habitat types as a result of hydrological differences. In frequently flooded habitats, for example, the soil seed bank might be replenished more often by propagules from local extant plant communities as these may have greater opportunity for reproductively successful recruitment events than those in rarely flooded areas (Capon & Brock 2006). A corollary of this however, is that soil seed banks in frequently flooded habitats may also lose more propagules as a result of more frequent germination events. Over longer distances, propagule dispersal is also likely to be influenced by hydrology (Nilsson *et al.* 1991; Nilsson *et al.* 2002) and additions due to hydrochory could be expected to decline with decreasing flood frequency. Loss of seeds through scouring of sediments, however, may be more common in frequently flooded habitats. Maximum seed abundance might therefore be expected to occur in soil seed banks of intermediately flooded habitats. It is also probable that the incorporation of seeds into soil seed banks depends partially on sediment characteristics, e.g. particle size and degree of compaction. As these often differ between hydro-geomorphic habitats, soil seed banks might be further differentiated spatially as a result.

This study indicates that the soil seed bank of the semi-arid Narran Lakes wetland system is indeed structured spatially at the scale of hydro-geomorphic riverine habitats and, furthermore, that hydrology is likely to be a major determinant of this variation. The abundance, richness and composition of the germinable soil seed bank all differed significantly between habitats with some degree of predictability and, as hypothesised, germinable seed abundance was greatest in intermediately flooded habitats. In the most frequently flooded habitats, the soil seed bank contained the least number of species and, as indicated by the ordination, tended to be compositionally similar amongst replicate samples, suggesting a potentially limited occurrence of species in the regional species pool capable of completing their life cycles under such hydrological conditions. Further support for this is the observation that, amongst the waterlogged samples, dominance tended to be highest in these habitats. Dominance by a few flood tolerant species in frequently flooded habitats has also been observed in other variable arid wetlands (Capon 2005). In contrast, the greatest species diversity, demonstrated by both high species richness and high numbers of unique species, was observed in the soil seed bank of the two floodplain habitats. In addition to being amongst the least frequently inundated habitats of those considered, it is also likely that the lignum and chenopod floodplains receive amongst the most variable within-habitat hydrological regimes with flood duration, depth and rates of drawdown varying considerably both temporally, between flood events, and spatially, between sites depending on microtopographical differences and lateral distance from the channel. The soil seed bank in these habitats therefore probably comprises suites of species which germinate in response to a much wider range of conditions including submergence as well as rainfall during dry periods. Species that are less competitive under submerged conditions that may have been excluded from more frequently flooded habitats could also contribute to the high species richness as might species which have been dispersed from upland systems adjacent to these peripheral wetland habitats (Capon & Brock 2006).

The results suggest that hydrology, and its interaction with geomorphology, also affect the degree of local variability in soil seed bank composition and structure. With the exception of the Narran River channel, the more frequently flooded habitats displayed relatively low variability in composition between replicates within sites and between sites within habitats. The local hydrological regimes (e.g. frequency, depth and duration of inundation) of these three lake habitats are likely to be relatively homogeneous at the within-habitat scale in contrast with the river channel, river bank and floodplain habitats within which microtopographical variations, as well as differences due to distance in the latter, are more extreme. Consequently, seeds are probably dispersed quite evenly by hydrochory in the lake habitat types (Haukos & Smith 1994). Conversely, replicates within sites and sites within habitats were considerably more heterogeneous in both the river channel and the least frequently flooded habitat types suggesting that factors not reflected at the broad hydro-geomorphic habitat scale, e.g. local soil characteristics, rainfall etc., play an important, although secondary, role in structuring soil seed bank composition amongst these habitats. Within the river channel, for instance, hydro-geomorphic processes are likely to vary quite significantly between pools and shallower intervening areas, potentially influencing localised patterns of seed bank depletion and replenishment and accounting for the greater variability in seed bank composition observed at the habitat scale.

In habitats dominated by perennial vegetation, spatial variability in the soil seed bank may also be governed by effects of shrubs or trees on both seed dispersal and subsequent germination and seedling survival (Pugnaire & Lazaro 2000). Dispersal might be influenced by vegetation through influences on vector movement, e.g. changes in water flow and turbulence close to shrubs, or seed capture and ingested seeds from birds may lead to a concentration of seeds in patches of vegetation as a result of perching and roosting preferences (Mull & MacMahon 1996). Environmental conditions beneath shrub cover, e.g. shading and enhanced organic matter and nutrient concentrations from leaf litter, may facilitate seedling survival in some species (Pugnaire *et al.* 1996; Moro *et al.* 1997) while germination and survival of others might be limited by competition or shading in such micro-habitats (Jensen & Gutekunst 2003).

This study has demonstrated that fluvial processes are a key determinant of spatial variability in soil seed bank composition and structure in the semi-arid Narran Lakes wetland system. While the results indicate that local factors are also likely to contribute to spatial patterns in soil seed banks, particularly in rarely inundated habitats, hydro-geomorphic habitat type appears to be a relatively strong predictor of the abundance, species richness and composition of the seed bank at the within-wetland scale in this heterogeneous system. Alterations to the spatial characteristics of the hydrological regime through upstream water resource developments or climate change could therefore be expected to be reflected by changes in soil seed bank composition and structure. In particular, a reduction in the occurrence of large flood events could result in a decline of species diversity in the soil seed bank of the infrequently inundated lignum and chenopod floodplains as hydrophytic species present in these habitats may become depleted through mortality or granivory without adequate opportunities to replenish their seed banks. Subsequent loss of local biodiversity and homogenisation of the soil seed bank at the habitat scale might also be expected to ensue in the long term as a result of anthropogenic reductions in flood frequency. As soil seed banks are a crucial means by which vegetation responds to flooding and drying in ephemeral wetlands, such effects would be likely to have far-reaching ecological consequences.

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Table 1 Major hydro-geomorphic habitats identified in the Narran Lakes Nature Reserve showing elevation, % time inundated in a 23 year period, flood duration and predominant perennial vegetation types. Habitats listed in order of decreasing flood frequency.

Habitat	Code	Elevation (m) (Mean ± standard deviation)	% Time inundated between 1981 and 2004[1]	Approximate duration (weeks) of inundation following single flood event [1]	Dominant perennial vegetation
Narran River	NRI	120.00 ± 0.04	70	24 - 48	None
Clear Lake	CLC	120.00 ± 0.10	42	24	None
Back Lake	BLC	120.32 ± 0.13	30	12	Lignum open shrubland
Clear Lake Shore	CLS	120.34 ± 0.20	28	2 – 4	Lignum open shrubland
Lignum Floodplain	LFP	120.67 ± 0.04	26	2	Lignum open shrubland
Narran River Bank	NRB	122.00 ± 0.54	21	1 – 2	Mixed open woodland
Chenopod Floodplain	CFP	122.21 ± 0.32	0[2]	< 1[2]	Chenopod open shrubland

[1] Data derived from inspection of a set of 70 Landsat MSS, TM, and ETM+ data from 1981 to 2004 including the before and after flood extents for every flood on the Narran River during this period and supported by inundation volumes and depths (derived from LiDAR data) and daily evaporation data from Walgett, NSW, approximately 75 km west of the Narran Lakes.

[2] Although not subjected to prolonged submergence, personal observations and anecdotal evidence suggest that sites on the chenopod floodplain are likely to experience some degree of wetting as a result of lateral water movement through the soil in association with large flood events.

Table 2 F ratios and probability values of mixed model ANOVA for seedling abundance (square root transformed), species richness, and the Berger-Parker dominance index (seedling abundance of dominant species/total seedling abundance).

Source		Species abundance		Seedling richness		Dominance	
	d.f.	*F*	*p*	*F*	*p*	*F*	*p*
Habitat	6	9.50	<.0001	19.96	<.0001	1.80	0.1216
Treatment	1	394.18	<.0001	522.85	<.0001	5.20	0.0277
Habitat x Treatment	6	6.34	0.0001	15.87	<.0001	1.10	0.3769
Site(Habitat)	14	3.58	0.0007	2.85	0.0044	1.32	0.2387
Treatment x Site(Habitat)	14	1.48	0.1597	1.49	0.159	1.91	0.0526
Replicate(Site(Habitat))	42	1.30	0.1986	1.33	0.1775	0.90	0.6261

Table 3 R values from two-way nested ANOSIM comparing similarities of plant assemblages within and between habitats. Pair-wise tests not shown all returned R values of 1.0. Global R (between sites) = 0.494, $p < 0.001$ and Global R (between habitats) = 0.682, $p < 0.001$ (1000 permutations). As only ten permutations are possible for pair-wise comparisons of habitats significance levels are set at $p = 0.1$.

Pair-wise test	R statistic
CLC vs BLC	0.926
CLC vs LFP	0.704
CLC vs NRI	0.259
CLS vs BLC	0.963
CLS vs LFP	0.481
CLS vs NRI	0.926
BLC vs LFP	0.444
BLC vs NR	0.815

Table 4 Significance of species vectors ($p \leq 0.05$) from PCC analysis determined using Monte Carlo randomisation technique (1000 permutations).

Code	Species	Significance
1	*Centrolepis polygyna* Hieron.	0.001
2	*Cyperus squarrosus* Rottb.	0.001
3	*Fimbristylis dichotoma* (L.) Vahl	0.001
4	*Triglochin calcitrapa* Hook.	0.001
5	*Dactyloctenium radulans* P.Beauv.	0.001
6	*Tripogon loliiformis* C.E.Hubb.	0.025
7	*Brachyscome goniocarpa* Sond.	0.01
8	*Epaltes australis* Less.	0.001
9	*Plagiobothrys plurisepaleus** (F.Muell.) I.M.Johnst.	0.001
10	*Hypericum gramineum* G.Forst.	0.05
11	*Calandrinia ptychosperma* S.Moore	0.001
12	*Eleocharis pusilla** R.Br.	0.025
13	*Calotis hispidula* F.Muell	0.05
14	*Bergia trimera* Fisch. & C.A.Mey	0.05
15	*Elacholoma hornii* F.Muell & Tate	0.05
16	*Glossostigma diandrum* (L.) Kuntze	0.05
17	*Cyperus bifax* C.B.Clarke	0.001
18	*Cyperus concinnus* R.Br.	0.001
19	*Juncus aridicola* L.A.S.Johnson	0.001
20	*Sporobolus caroli* Mez	0.001
21	*Gamochaeta calviceps* (Fernald) Cabrera	0.001
22	*Euchiton sphaericum* (Willd.) Holub	0.01

23	*Ammannia multiflora* Roxb.	0.001
24	*Sporobolus mitchelli** S.T.Blake	0.01
25	*Haloragis glauca* Lindl.	0.05
26	*Ranunculus pendandrus var. platycarpus* J.M.Black	0.001
27	*Rorippa eustylis** (F.Muell.) L.A.S.Johnson	0.05
28	*Heliotropium supinum* L.	0.025
29	*Centaurium spicatum* (L.) Fritsch	0.001
30	*Lythrum wilsonii* Hewson	0.01
31	*Gnaphalium polycaulon* Pers.	0.001
32	*Cyperus pygmaeus* Rottb.	0.01
33	*Centipeda cunninghamii* A.Braun & Asch.	0.001
34	*Trigonella suavissima* Lindl.	0.001
35	*Cullen cinereum* (Lindl.) J.W.Grimes	0.01
36	*Myriophyllum verrucosum* Lindl.	0.025
37	*Polygonum plebeium* R.Br.	0.001
38	*Calotis scapigera* Hook.	0.025
39	*Cyperus gymnocaulos* Steud.	0.01

* Species not confirmed from herbarium samples as samples immature

Figure headings

Fig. 1 Map of Narran Lakes. Shaded area indicates Nature Reserve. Inset shows Condamine-Balonne river basin.

Fig. 2 Mean monthly temperatures (°C) and precipitation (mm) at Walgett (30° 15’ S, 148° 07’ E).

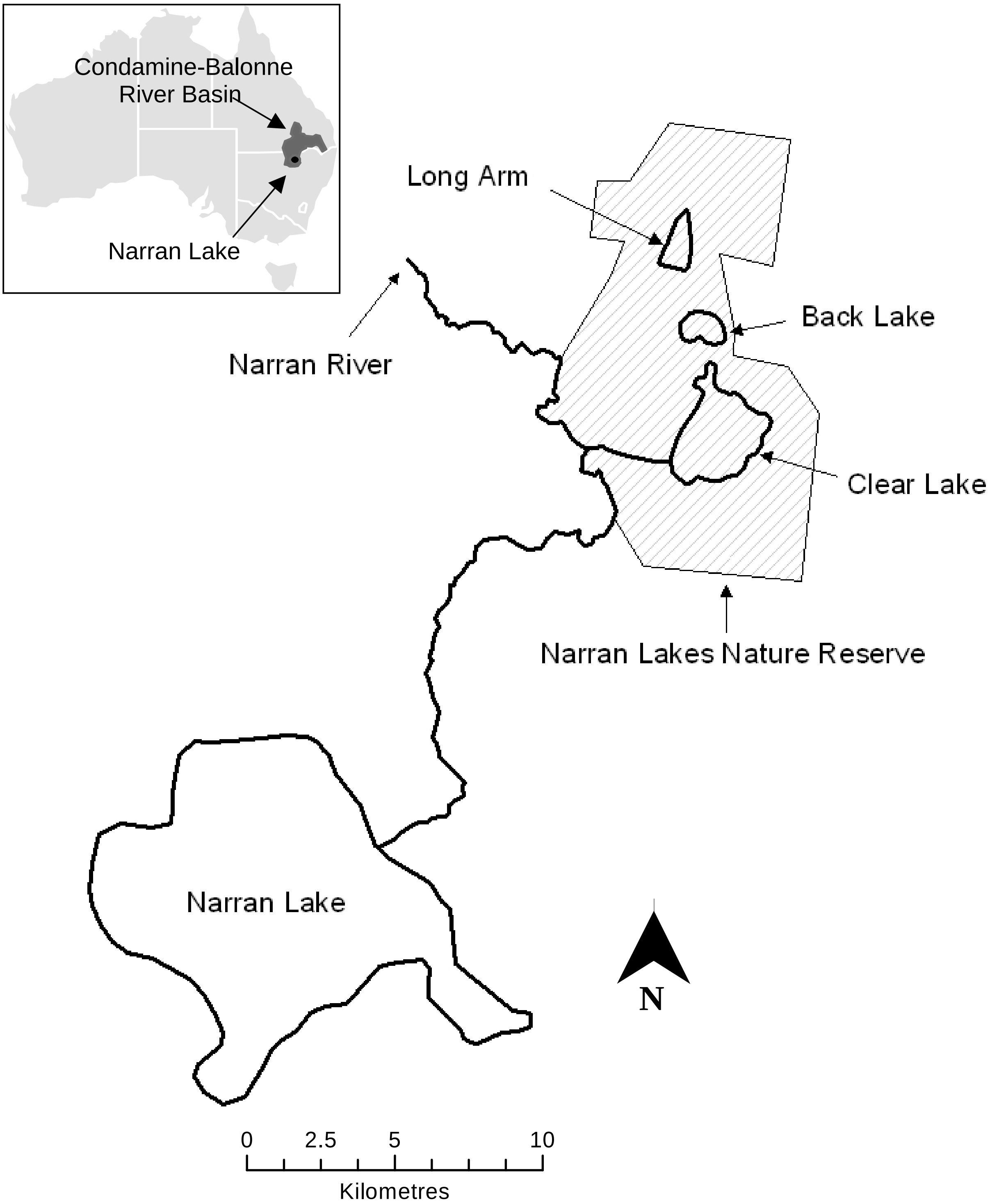
Fig. 3 Annual discharge of the Narran River at Wilby Wilby gauging station, approximately 80 km upstream of the Narran Lakes Nature Reserve, between 1965 and 2004.

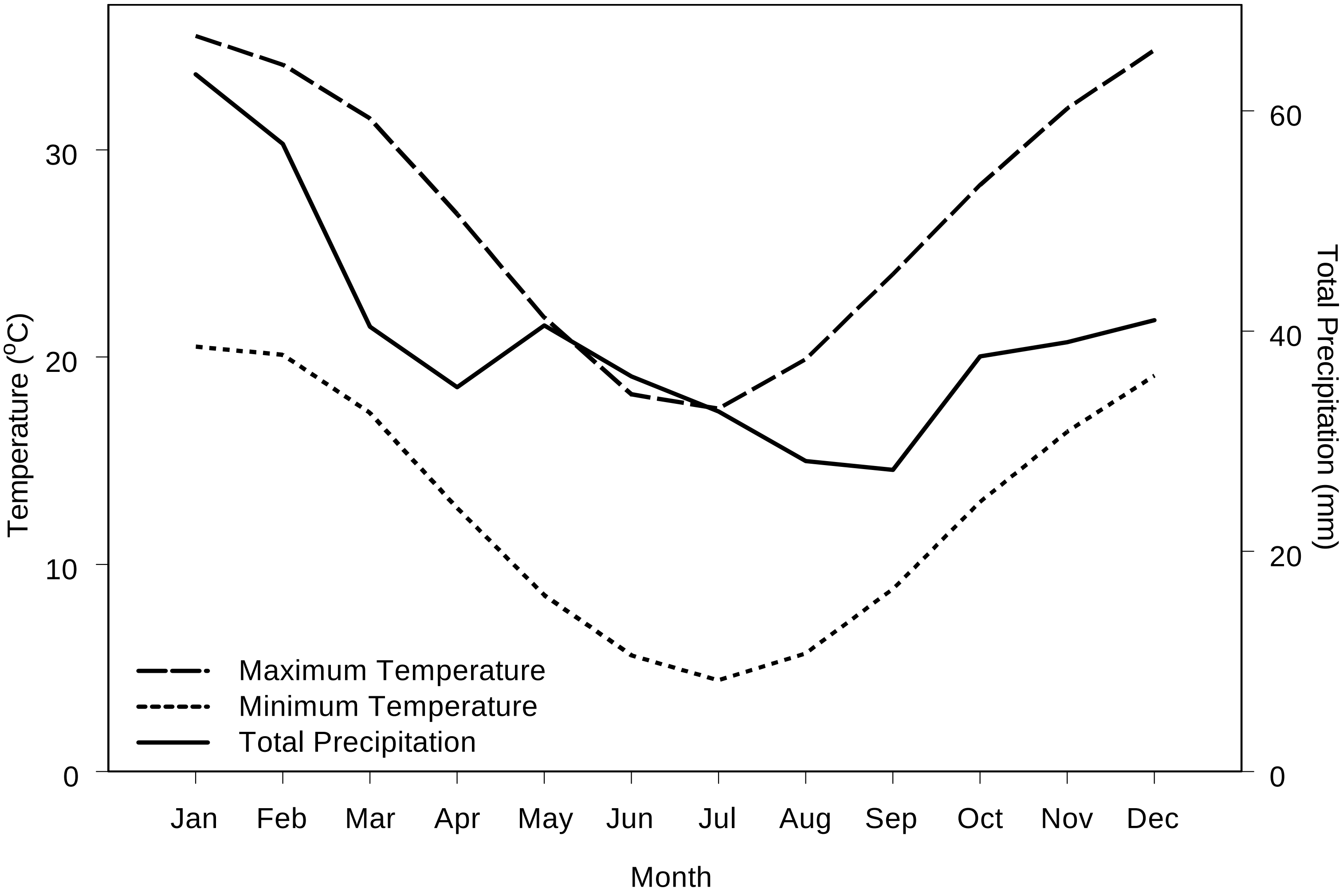
Fig. 4 Mean seedling abundance (a) and species richness (b) of plants germinating from waterlogged (■) and submerged (▨) sediments collected from seven hydro-geomorphic habitats. Values are means ± standard errors. (Habitat codes are described in Table 1)

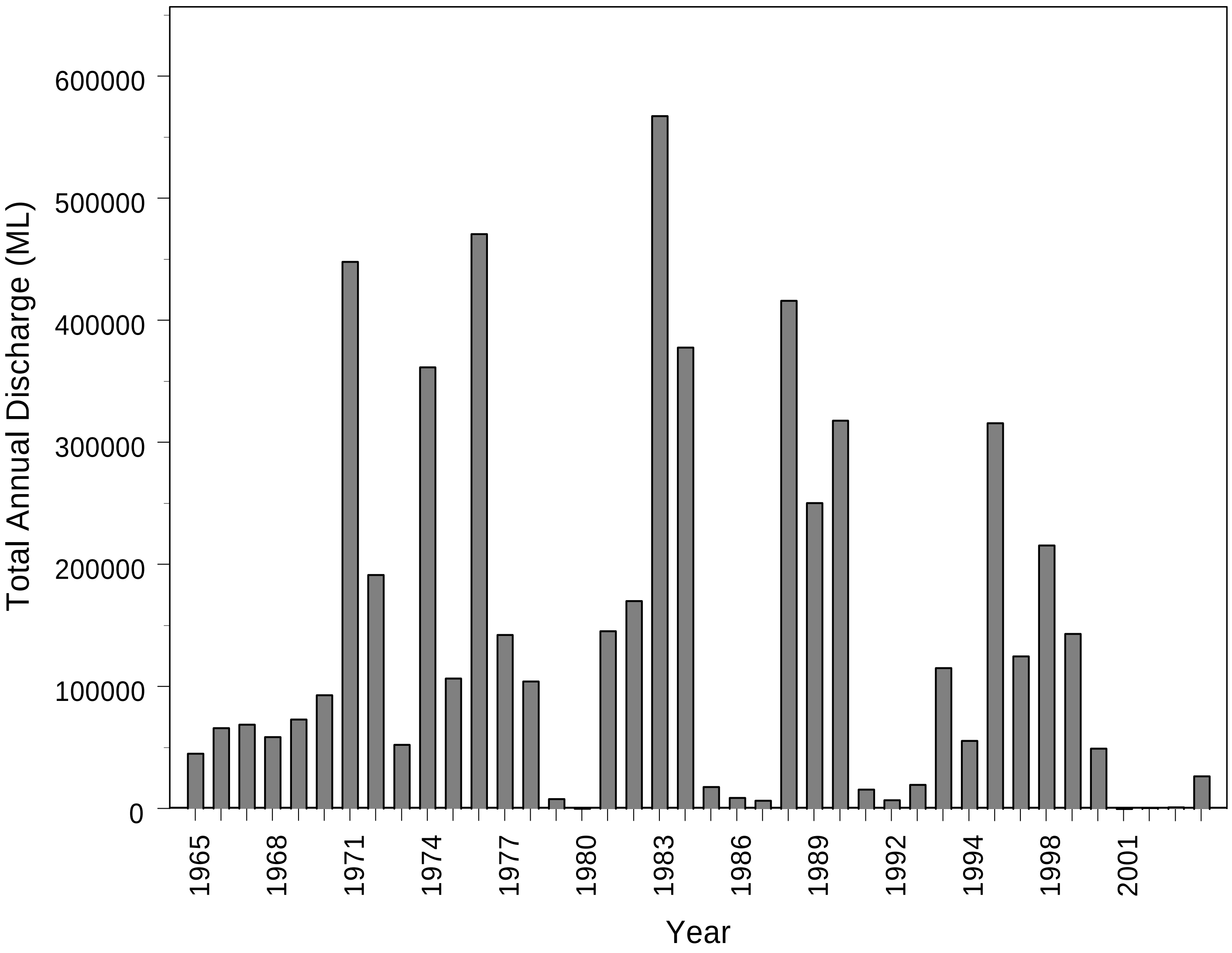
Fig. 5 (a) Mean Berger-Parker dominance (means ± standard errors) of plants germinating from waterlogged (■) and submerged (▨) sediments and, (b) numbers of singlet (■) (species occurring in only one habitat) and doublet (□) (species occurring in only two habitats) plant species germinating from sediments collected from seven hydro-geomorphic habitats. (Habitat codes are described in Table 1)

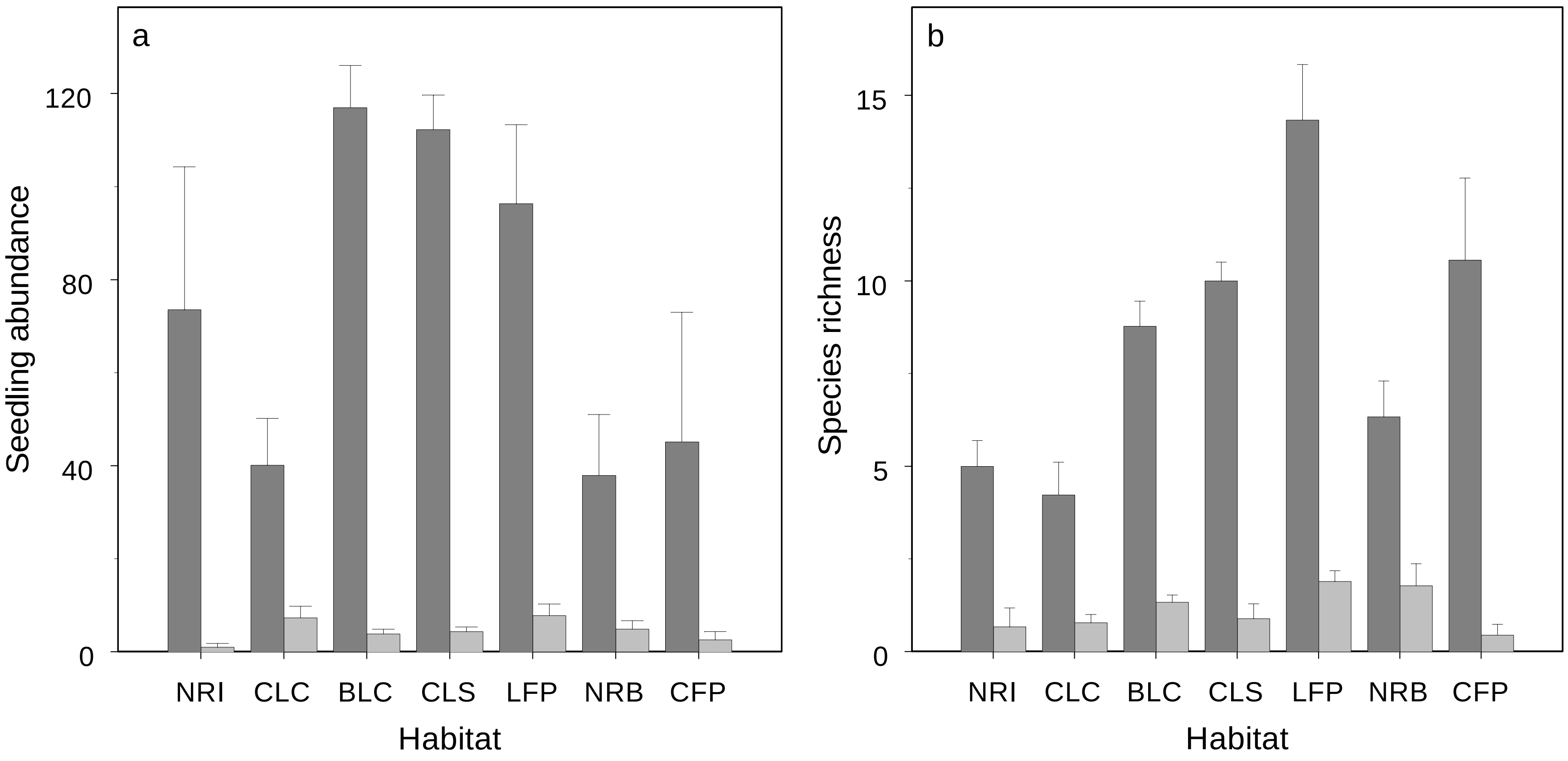
Fig. 6 nMDS ordination plots based on species abundances in waterlogged treatment showing (a) replicates within habitats and (b) species vectors. Stress = 0.125, axes 1 and 3 are shown as these explained the greatest variation. Species’ PCC vectors are those significantly correlated ($P \leq 0.05$) with the nMDS ordination axes. Habitat codes are described in Table 1 and species numerical codes are given in Table 4.

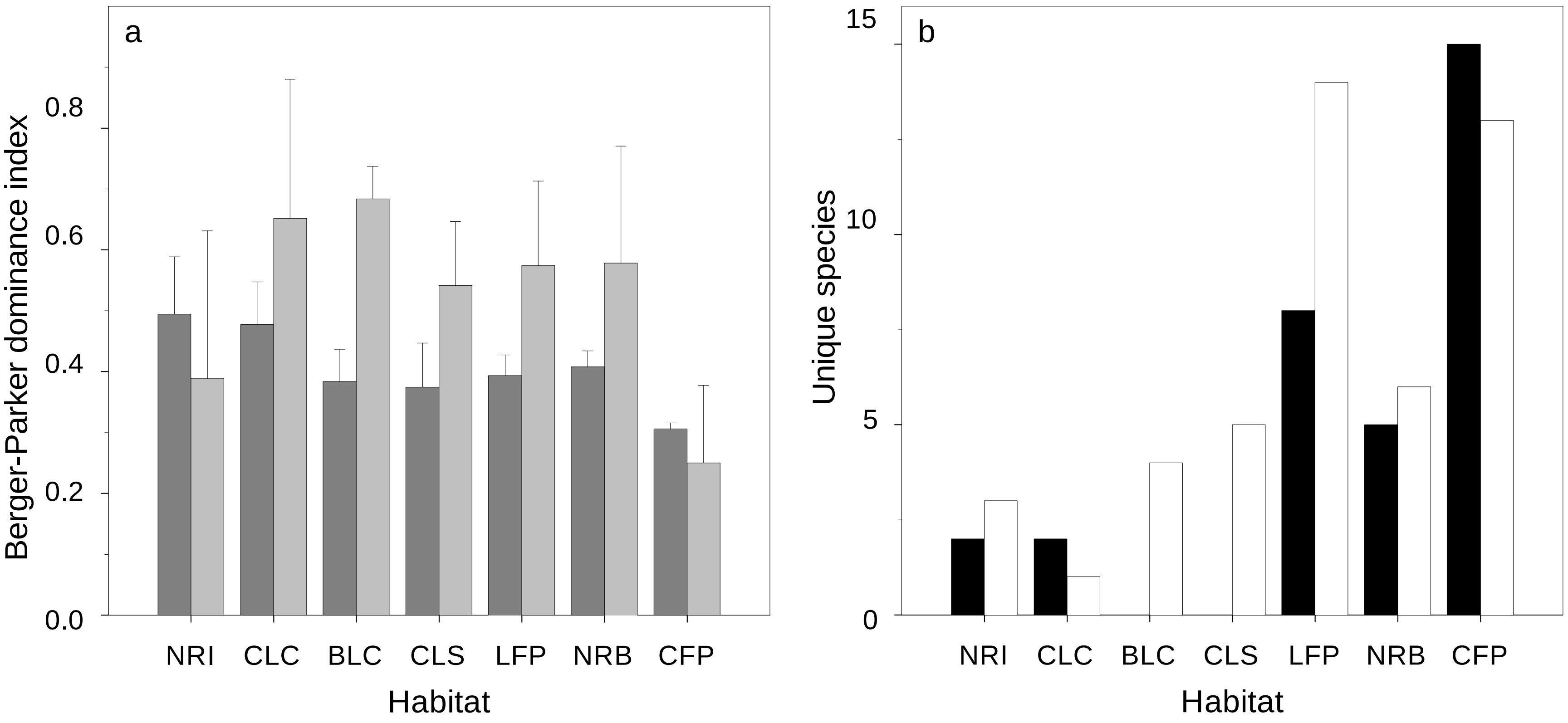
Fig. 7 Box plots of Bray-Curtis dissimilarity scores for pair-wise comparisons between replicates nested within sites (a) and sites nested within habitats (b).

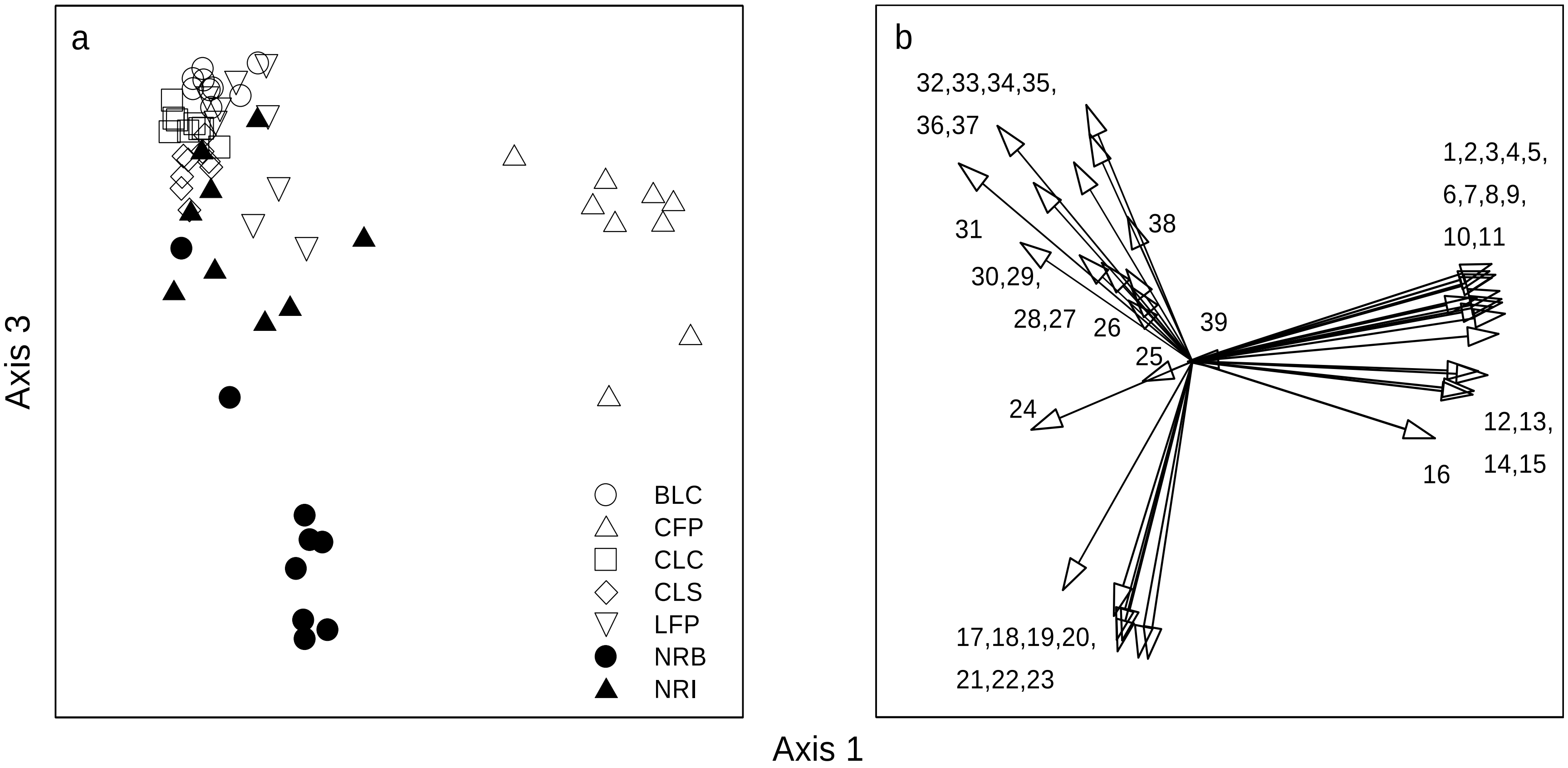

Condamine-Balonne
River Basin
Narran Lake
Long Arm
Back Lake
Narran River
Clear Lake
Narran Lakes Nature Reserve
Narran Lake
N
0
2.5
5
10
Kilometres

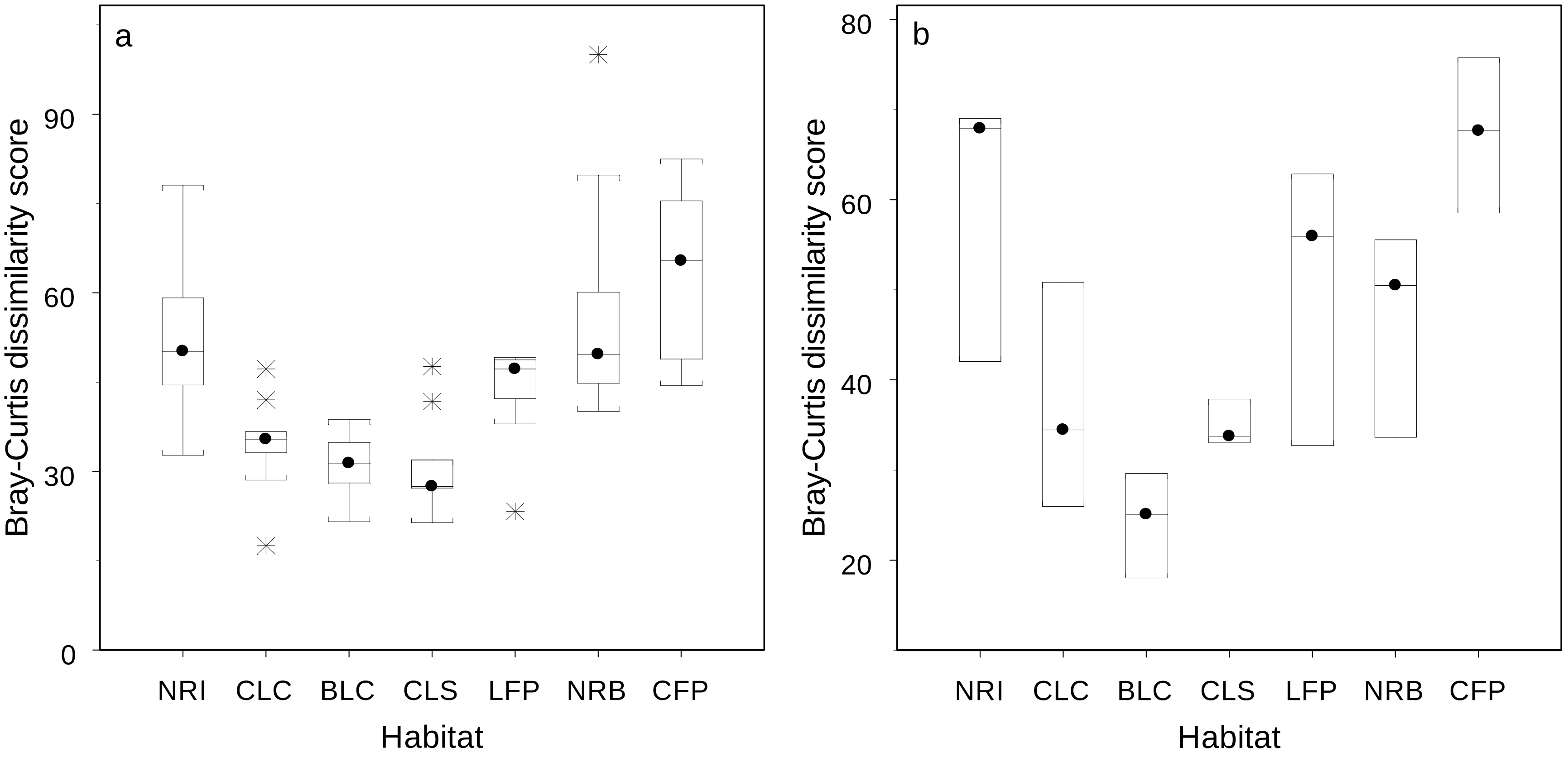

Temperature (°C)
0
10
20
30
Total Precipitation (mm)
0
20
40
60
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month
Maximum Temperature
Minimum Temperature
Total Precipitation


Total Annual Discharge (ML)
600000
500000
400000
300000
200000
100000
0
1965
1968
1971
1974
1977
1980
1983
1986
1989
1992
1994
1998
2001
Year


a
Seedling abundance
120
80
40
0
NRI
CLC
BLC
CLS
LFP
NRB
CFP
Habitat
b
Species richness
15
10
5
0
NRI
CLC
BLC
CLS
LFP
NRB
CFP
Habitat


a
Berger-Parker dominance index
0.0
0.2
0.4
0.6
0.8
NRI
CLC
BLC
CLS
LFP
NRB
CFP
Habitat
b
Unique species
0
5
10
15
NRI
CLC
BLC
CLS
LFP
NRB
CFP
Habitat


a
BLC
CFP
CLC
CLS
LFP
NRB
NRI
b
32,33,34,35,
36,37
31
30,29,
28,27
26
25
24
38
39
1,2,3,4,5,
6,7,8,9,
10,11
12,13,
14,15
16
17,18,19,20,
21,22,23
Axis 3
Axis 1


a
Bray-Curtis dissimilarity score
0
30
60
90
NRI
CLC
BLC
CLS
LFP
NRB
CFP
Habitat
b
Bray-Curtis dissimilarity score
20
40
60
80
NRI
CLC
BLC
CLS
LFP
NRB
CFP
Habitat