Title: Species and environmental characteristics point to flow regulation and drought as drivers of riparian plant invasion

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(A) Summary

Aim: Many factors facilitate biological invasions, making it difficult to determine their relative importance, especially when relying on survey data that include confounded variables. Incorporating information about species characteristics can improve inferences drawn from species-environment relationships, which can inform management. We seek to understand why the abundance of exotic, and not native, terrestrial plants is higher in riparian wetlands most impacted by flow regulation.

Location: River Murray, SE Australia.

Methods: We use variance-components analysis and hierarchical generalised linear models to examine whether the positive relationship between flow regulation and proportional cover of exotic plants is driven by altered hydrological regimes, wetland drying and drought, superior colonisation ability of exotic species following disturbance or human-elevated propagule pressure.

Results: Of the four hypotheses, hydrological modification (indicated by flood magnitude) most likely drives invasion. Flow regulation may inhibit native species adapted to the historical hydrological regime, facilitating exotic species with different environmental ranges. A symptom of environmental change, invasion may have been exacerbated by drought, though it is unclear why.

There was no indication that human-elevated propagule pressure or colonisation ability facilitated invasion. Exotic cover was unrelated to proximity to towns, recent flood frequency and cattle grazing intensity. Additionally, similar proportions of exotic and native species were used in cultivation and, despite a higher proportion of exotics being known weeds, weed status was unrelated to exotic species occupancy. Overall, colonisation ability was unrelated to species' origin or response to water depth and hydrological change. Although exotics had higher specific leaf area and shorter longevity (indicative of higher colonisation ability), they had heavier (not lighter) seeds and did not differ in height from natives.

Main conclusions: Using environmental flows to reinstate mid-range floods and augmenting the propagule supply of native species with characteristics suitable for modified conditions may help limit invasion in these wetlands.

Keywords: disturbance regime; environmental flows; floodplain wetlands; functional traits; invasive alien species; weed management

(A) Introduction

Biological invasion is a function of invader propagule availability, local environmental conditions and interactions between the invader and recipient community (Catford *et al.* 2009). Determining the relative importance of these factors is crucial for identifying the most effective way to limit and manage invasion. However, given the complexity of the invasion process, this goal can be difficult, especially for widespread invasions, like those along rivers. Such investigations generally rely on survey data because of an inability to conduct large-scale, long-term multi-factorial experiments using exotic, and potentially invasive, species. Because surveys deliver correlations that often use confounded variables, strong inference of cause and effect from surveys is limited (Downes *et al.* 2002). Incorporating data about species characteristics into survey-based approaches provides an additional line of evidence that can be used to improve inferences drawn from patterns (Lasky *et al.* 2013). In this paper, we illustrate how using information about environmental gradients, species distributions and species characteristics can increase understanding of ecological phenomena – here, riparian plant invasion, which can help inform management responses.

Numerous hypotheses have been proposed to explain the high level of exotic invasion observed in riparian ecosystems worldwide (Richardson *et al.* 2007). The composition of riparian plant communities is strongly influenced by river flow regimes, so hydrological modification is a leading explanation for both the addition and loss of species (Dynesius *et al.* 2004; Merritt *et al.* 2010). In a previous study centred around floodplain wetlands, Catford *et al.* (2011) hypothesised that, by collectively altering the frequency, timing, duration, magnitude and predictability of flooding and drawdown, flow regulation could potentially facilitate invasion by: a) prompting a decline in native species adapted to the historical hydrological regime, allowing species with broader environmental ranges to increase in abundance; and/or b) providing conditions that favour exotic species pre-adapted to the altered conditions. Based on trends in extant vegetation, Catford *et al.* (2011) concluded that hydrological modification led to an increase in terrestrial species and a decline in aquatic and semi-aquatic ones (the vast majority of which were native) along the River Murray, Australia. However, only terrestrial exotics increased in abundance whereas terrestrial natives did not, suggesting factors other than solely hydrological modification might be at play (i.e. the observed relationship between terrestrial exotic cover and hydrological modification may be correlative, not causal). Species origin has similarly been found to modulate species' responses to grazing pressure (Dorrough and Scroggie 2008); also in south-eastern Australia, Dorrough and Scroggie (2008) found that the occupancy of native annual and perennial herbs declined with increasing grazing pressure, but the occupancy of their exotic counterparts was unaffected.

Notwithstanding the original hypotheses that hydrological modification prompted changes in wetland flora, Catford *et al.* (2011) suggested that the exotic terrestrial species may have been favoured by elevated propagule pressure around centres of human activity. Humans can give some species a storage and dispersal advantage by planting them in high numbers (Dehnen-Schmutz *et al.* 2007) and, often unintentionally, transporting them around the landscape (Taylor *et al.* 2012). If exotic species have a closer association with humans than native species (e.g. cultivated more frequently), this could increase their propagule availability in a way that is independent of their physiological characteristics (or at least partially, von der Lippe and Kowarik 2012). High propagule availability can increase colonisation success across all environmental conditions, but it is particularly influential in areas with high resource availability (Catford *et al.* 2012), which might occur if the abundance of, and uptake by, natives species declines (Davis *et al.* 2000).

Working in a similar river system, Lunt *et al.* (2012) posited a different explanation for the higher performance of exotic species as a group: their higher colonisation ability, including their annual life history, enabled them to rapidly colonise areas once floodwater receded. If this is correct, we would not only expect exotic species to have superior colonisation ability (indicated by an overrepresentation of species with a high specific leaf area, short stature, small seed mass and an annual life history; Cornelissen *et al.* 2003; Besaw *et al.* 2011), but we would expect that species with these characteristics would be more common in highly disturbed areas and wetlands most impacted by flow regulation.

There are thus three distinct (though not mutually exclusive) explanations for the disproportional increase in exotic plant abundance observed along the River Murray:

Hypothesis 1 – Superior adaptation of exotic species to the modified hydrological regime;

Hypothesis 2 – Human-mediated dispersal and broad scale planting of exotic species increases their propagule pressure relative to natives; and

Hypothesis 3 – Higher colonisation ability of exotic species group enables niche pre-emption after disturbance.

To these we add a fourth:

Hypothesis 4 – Superior adaptation of exotic species to dry conditions.

It is plausible that a net reduction in river discharge (i.e. overall water availability) rather than the more nuanced effects of regime change (e.g. changes in flood timing) drives the association between exotic cover and hydrological modification, as seen in systems experiencing “terrestrialisation” (Poff and Zimmerman 2010). If exotics are better able to withstand the environmental stress associated with drying, we would expect that, compared to native species, more exotic species would have a perennial life history (Pérez-Harguindeguy *et al.* 2013), a large seed mass (Moles and Westoby 2004) and would germinate on dry, rather than saturated, soil (Brock and Casanova 1997).

The effect of drying could be compounded by drought, a severe one of which occurred in the study region at the time of Catford *et al.*'s (2011) survey. Given the naturally high occurrence of drought in Australia (CSIRO 2008), we think it unlikely that exotic species would be better adapted to dry conditions than native species. However, river regulation in semi-arid and arid regions around the world has been accompanied by invasion of drought-tolerant species (Kominoski *et al.* 2013) and it has been suggested that climate change, including reductions in rainfall and increased occurrence of drought, may facilitate the spread of exotic species because of e.g. their broader environmental ranges and greater plasticity (Walther *et al.* 2009; see references in Catford *et al.* 2013).

We investigate the relative support for these four hypotheses in River Murray wetlands using three lines of evidence (Table 1). First, we test whether proportional exotic plant cover is related to impacts of flow regulation (Hypothesis 1, H1), proximity to human activities (H2), disturbance from floods and livestock grazing (H2), and depth of standing water and soil moisture (H4). Second, we examine whether the exotic and native species groups differ in their values of seven characteristics that are thought to relate to Hypotheses 2, 3 and 4 (weed of agriculture or disturbed areas, cultivated or planted as an ornamental, longevity, plant height, seed mass, specific leaf area, germination requirements). Third, we investigate whether species occupancy along environmental gradients varies as a function of these seven characteristics.

Because of the multi-faceted nature of flow regime change, it is hard to identify species characteristics that would relate to hydrological modification as a whole (Casanova 2011). For example, species characteristics that relate to changes in flood timing (e.g. time of flowering) are unlikely to relate to changes in flood duration (e.g. adaptation to anaerobic conditions). We are thus unable to directly test whether exotics are better adapted to the modified flow regime than native species. However, our approach allows us to evaluate the three other likely explanations for invasion in this system. All of our tests reflect our interest in explaining patterns in extant vegetation and hence do not consider persistence in the soil seedbank.

(A) Methods

(B) Study region, hydrological modification and drought

Surveys were conducted in 24 temporary floodplain wetlands (sedge-dominated depressions largely free of woody vegetation) along a contiguous 398 km long stretch of the River Murray between Albury and Barmah in temperate south-eastern Australia (see Fig. S1 in Supporting Information). Additional information about the study wetlands and region are provided in Appendix S1.

Regulated since the late 1800s, 90-98% of diverted water from the river is used for summer irrigation, which has prompted an overall decline in winter and spring flows and an increase in summer and autumn flows (Maheshwari *et al.* 1995). Large infrequent floods (>40 to 50 years average return interval, ARI) have not been altered by regulation, but small- and mid-size floods are now less frequent, e.g. floods that previously had a 2 year and a 20 year ARI now have a 5 year and 32 year ARI respectively (Catford *et al.* 2011; see Appendix S2 for more detail). Mid-range floods (10-20 year ARI) have been most affected by regulation (Maheshwari *et al.* 1995). The furthest upstream wetlands are just downstream of a major dam (Hume Dam). Effects of regulation generally decrease with distance downstream, largely because of inflows from unregulated tributaries. However, because of differences in wetland geomorphology and elevation, changes in wetland hydrology are not entirely linked with wetland location (Pearson's r = 0.765, Table S1).

The survey period (13 Dec. 2005 – 4 Feb. 2006) coincided with a severe drought in south-eastern Australia that extended from 1997 to 2009 (LeBlanc *et al.* 2012). It was the second most severe drought in the region between 1910 and 2005 and was exacerbated by flow regulation (see Appendix S3). Although annual rainfall between 1889 and 2005 was similar across the study region, the period between floods became longer than normal leading up to the end of 2005. Mean annual flow (MAF) was close to average in 2005, but MAF for the period 1997 – 2005 was 45% lower than MAF for 1910 – 2005.

(B) Floristic survey and species characteristics

Described previously (Catford and Downes 2010), wetlands were surveyed in the austral summer using a stratified random approach. In each of three strata, which were based on elevation, foliar cover of all plant taxa was estimated in 1 m^2 quadrats at 8 random points using the Braun-Blanquet scale (converted to mid-point averages for analysis). Data from the three strata were given equal weight despite differences in areal extent.

Of 157 taxa recorded, 127 were identified to species-level, 139 to genera and 148 to family (authority: Botanic Gardens Trust 2007). Cover of all unidentified plant taxa (mostly daisies, grasses and seedlings) made up less than 6% of wetland vegetation cover (mean = 1.8%).

Of 57 exotic species recorded, 51 were classified as terrestrial (i.e. species that inhabit dry areas of wetlands where the water table is below the soil surface or the soil is saturated; Brock and Casanova 1997), whereas natives were more evenly split (49 terrestrial, 38 semi-aquatic). Reflecting the study aims, analyses only include terrestrial species (i.e. all aquatic and semi-aquatic species excluded).

Species (exotic and native) were classified based on their germination requirements (i.e. whether species germinate on saturated soil ("damp germinants") or dry soil ("dry germinants"); Brock and Casanova 1997; Table S3), geographic origin (exotic or native to Australia), longevity (annual and biennial versus perennial; Botanic Gardens Trust 2007), weed status (i.e. any exotic and native species that are weeds of agriculture and disturbed areas anywhere in the world, Randall 2007) and whether they are cultivated or used as ornamentals (see Appendix S4 for weed and cultivation classification procedure).

Information about species' seed mass was sourced from available databases (Liu *et al.* 2008) and field collections (9 species). Specific leaf area (SLA) was measured on an average of 13 leaves (6 leaves minimum) from at least two different plants for each species following Cornelissen *et al.* (2003). Leaves were collected in January 2012 from wetlands in the centre of the study region. We used single-sided scans of leaf blades for grasses and of green stems for rushes and sedges. We measured larger leaves with a LI-3000C Portable Leaf Area Meter (LI-COR Biosciences, Lincoln, NE, USA) and small leaves with ImageJ (http://rsb.info.nih.gov/ij/). Where trait data were unavailable, the mean value from as many congeners as possible was used (seed mass estimated for 14 species, SLA estimated for 22 species). Trait data were available for 36 native and 40 exotic terrestrial plant species, which collectively accounted for a mean of 88% of total terrestrial cover across all wetlands (3% standard error).

(B) Environmental variables

We used six environmental variables to test our hypotheses (Table 1): change in maximum flood magnitude to represent hydrological change; water depth and soil moisture content to represent wetland drying; recent flood frequency and cattle pugs (footprints) to represent recent episodic disturbance; and proximity to the nearest town to represent strength of human association. We use a space-for-time approach, where wetlands or quadrats form points along environmental gradients, to examine the potential influence of changes in these environmental variables on wetland flora. Site was included to account for unexplained variance at the wetland-scale.

Change in maximum flood magnitude is the difference in the magnitude (or depth) of the largest flood that would have occurred under pre- versus post-regulation conditions during the decade preceding the floristic surveys (1996-2006). Between 1996 and 2006, the largest flow event in the study region corresponded with a mid-range flood (namely, flow magnitudes of 8.5-18 year ARI under pre-regulation conditions; Catford *et al.* 2011). We used change in flood magnitude to represent hydrological change because it was strongly correlated (and was the variable most frequently correlated) with other aspects of hydrological modification (i.e. changes in flow timing, duration and variability and the number of times wetlands were inundated by the river) and was the hydrological change variable most strongly linked with exotic and native species cover (Catford *et al.* 2011). Preliminary analyses revealed that the inclusion of other variables relating to hydrological modification (e.g. change in flood timing and duration) did not increase our ability to explain trends in terrestrial exotic cover.

Described by Catford *et al.* (2011), we calculated change in maximum flood magnitude by generating daily time-step wetland water balance models under pre- and post-regulation conditions using simulated daily river flow data (MSM-BigMod, River Murray Water; MDBC 2002). The simulated river flow data effectively allows water levels of the river, with and without regulatory structures and water diversion, to be compared in real time. Using the modelled daily wetland water levels, flood depth was calculated under pre- and post-regulation scenarios and the extent of change in depth was represented by:

$$\text{Hydrological change} = \log_{10}[(\text{post} + 0.01) / (\text{pre} + 0.01)]$$

where post indicates post-regulation values and pre indicates pre-regulation values.

Water depth, if water was present, was measured at the centre of each quadrat (24 quadrats/wetland). Mean wetland percentage soil fresh moisture content was determined by comparing the wet and dry weights of ~60 g of sediment collected from six random points in each wetland (two samples/stratum, top 10 cm) following standard methods (Rayment and Higginson 1992; samples dried to a constant weight in Axyos Drying Oven, Gallay Scientific).

Flood frequency, defined as the number of inundation events between 1990 and 2000, was based on wetland-specific statistics generated through modelling (Catford *et al.* 2011). Flood frequency does not indicate hydrological change: it is based on recent flood history, not changes in flood history that result from regulation, and – because of differences in wetland characteristics – it is not necessarily correlated with flow regulation impacts. As for vegetation, recent disturbance from cattle was quantified by estimating the proportion of quadrats containing cattle pugs (Catford and Downes 2010).

Town proximity is the minimum distance between a wetland and the nearest town. Town proximity was quantified using maps and a floodplain digital elevation model.

Wetland proximity to towns was highly correlated with other measures of human activity [Pearson's r between wetlands' distance to nearest town and distance to closest: sealed road = 0.885; park boundary (usually the edge of agriculture) = 0.851; human dwelling = 0.843], so provides a general indicator of the likely strength of human activity.

Previous work in these wetlands indicated that proportional exotic plant cover was unrelated to soil nutrient levels, water chemistry, bathymetric variability (surrogate for habitat heterogeneity), hydraulic connectivity among wetlands and hydrochory (Catford 2008; Catford and Downes 2010).

(B) Statistical analysis

(C) Test 1: Variation in exotic cover

We used variance components analysis to examine relationships between environmental gradients and proportional exotic cover. Following the methods of Hector *et al.* (2011) and Gelman (2005), we built a hierarchical (multi-level) linear model where the response was the proportion of terrestrial plant cover in a quadrat that was exotic. Water depth and degree of cattle pugging were assessed at the quadrat level, whereas hydrological change, flood frequency, soil moisture and proximity to town were assessed at the wetland level. We consider important variance components as being those that account for at least 0.5 standard deviations of the total variance (median of posterior densities, Cohen 1988). We examined collinearity among environmental gradients (variables considered correlated if Pearson correlation coefficients ≥0.4).

(C) *Test 2: Species characteristics of the exotic and native species groups*

For the four binary species characteristics, we compared the proportions of the exotic and native species groups that fell into each category. For the three continuous species characteristics (SLA, plant height, seed mass), we estimated their means and variances and simulated approximate Bayesian 95% credible intervals for each probability density using point estimates and standard errors of log-transformed data. We examined correlations among the seven characteristics (Tables S4, S5 and S6).

(C) *Test 3: Species occupancy along environmental gradients*

If species characteristics influence the likelihood of species occupying areas with particular environmental conditions, the presence or absence of a given species should accord with that species' characteristics. If high SLA, for example, increases the probability of a species occupying a highly disturbed site, then SLA should interact positively with disturbance to explain species occupancy. If exotics differ from natives in the values and distributions of their characteristics (Test 2) and these characteristics affect how species respond to certain environmental gradients (Test 3), this may provide an explanation of why proportional exotic cover is higher in certain wetlands (Test 1).

We built a hierarchical generalised linear model of species occupancy as a function of environmental variables and mean values of seven species' characteristics (Pollock *et al.* 2012). Reflecting our interest in overall invasion rather than invasion of individual species, we restricted the analysis to environmental variables found important in Test 1. Separate models were fit for 76 terrestrial species for which we had presence-absence and species characteristics data. The response was the logit probability of species occupancy in a quadrat. The hierarchical approach allows species' response to environmental variables to vary.

We considered species characteristics to have an effect if their 95% credible intervals do not include zero and effect size of parameter estimate ± 0.5 standard deviations (SD). The coefficients for the native and exotic groups were compared by calculating the distribution of differences resulting from random draws from the respective posterior distributions. These expected differences between the coefficients for the native and exotic groups were then summarised as mean and 95% credible interval. We considered species origin to have an effect when mean differences were ±0.5 SD and 95% credible intervals did not include zero.

We found in favour of a particular hypothesis if Test 1, or Tests 2 and 3, or all tests supported it. All analysis was done using R version 3.0.1 (R Core Team 2012; description of analyses and R code in Appendix S5).

(A) Results

Exotic species contributed 1-52% of total vegetation cover and 3-71% of terrestrial vegetation cover in the wetlands (Table S2). The vast majority of wetland taxa were herbaceous (see full list of taxa in Table S1 of Catford *et al.* 2011). Terrestrial exotic and native species represented 28 families. Additional information on wetland flora is provided in Table S3, Downes and Catford (2010) and Catford *et al.* (2011).

(B) Test 1: Variation in exotic cover

Of the six environmental gradients examined in the variance components analysis, proportional exotic cover appeared to be most strongly linked with hydrological change (Fig. 1; Site accounted for the second greatest amount of variance). Consistent with Hypothesis 1 (H1, hydrological change), wetlands that had experienced the greatest reduction in flood magnitude because of regulation had higher proportional cover of exotic plants (Fig. 2a). In support of H4 (wetland drying), proportional exotic cover was higher in quadrats with less standing water (Figs 1 and 2b; NB. all analyses based on the terrestrial component of vegetation). Relationships with soil moisture suggest the same trends, but they are highly uncertain, so we do not examine them further (Figs 1 & 2c). Hydrological change and water depth were not correlated (r = 0.026; nor were hydrological change and soil moisture, r = -0.073; Table S1), indicating that their relationships with proportional exotic cover were independent.

Proximity to town and flood frequency did not explain any variance in proportional exotic cover with certainty (Figs 1, 2e & 2f) despite being positively correlated with hydrological change (town: r = 0.489, flood frequency: r = 0.545, Table S1). Proportional exotic cover did not vary with cattle pugging either and cattle pugging was not correlated with hydrological change (r = 0.286, Fig. 2d).

This first piece of evidence thus found strong support for H1 (hydrological change), moderate support for H4 (drying), but no support for H2 or H3 (human-elevated propagule pressure and colonisation ability, Table 2).

(B) Test 2: Species characteristics of the exotic and native species groups

Based on values of species characteristics, we found partial support for H2 (human-elevated propagule pressure) where one of two tests supported the hypothesis, and mixed support for H3 (colonisation ability) and H4 (drying; Table 2) where some of the results supported the hypotheses but others refuted them (and some showed no trends). Compared to the native species pool, more of the exotic species were classified as weeds (65% vs 20%), which is consistent with H2. However, no trends were found in relation to cultivation: similar proportions of exotic and native species are used in cultivation or as ornamentals (51% and 41% respectively, Table S7). The dominance of annual and biennials in the exotic species pool supports H3, as does their higher SLA, but the overall greater seed mass of exotics contradicts it (Figs 3a & 3c). Exotic and native species groups did not differ in plant height (Fig. 3b). Consistent with H4, more exotic species germinate on dry soil (61% vs 41%) and have heavier seeds than native species (Fig. 3c). However, unlike natives, exotic species were mostly annual or biennial (67% vs 24%), which contradicts H4.

(B) Test 3: Species occupancy along environmental gradients

We only examine responses to hydrological change and water depth because these were the only environmental gradients that were clearly linked with overall invasion level (Test 1, Figs 1 & 2).

The main effects illustrate that the occupancy of native species declined with increasing levels of hydrological change, whereas exotic species occupancy was unaffected by hydrological change (Figs 4 and S2, Table S8). This was the only response where trends in exotic and native species occupancy were markedly distinct (i.e. credible intervals did not overlap zero), as indicated by an expected mean difference of 1.78 SD (95% CI: 0.43, 3.22) between the parameter estimates for the native and exotic groups (Fig. 4, Table S9).

Based on results of Test 3, there is no evidence to suggest that human-elevated propagule pressure, exotics’ superior colonisation ability or wetland drying (H2, H3 and H4 respectively) drive the increase in proportional exotic cover with hydrological change (Table 2). The lower occupancy of cultivated exotic species with increasing levels of hydrological change contradicts H2. Similarly, the occupancy of native dry germinants declined with increasing hydrological change (Fig. 4), which contradicts H4. Differences in species' responses to hydrological change and water depth based on their characteristics also suggest that hydrological change and depth have different effects (i.e. elicit different responses) on species occupancy (e.g. compare effects of germination niche and SLA on native species occupancy along these two environmental gradients, Fig. 4). No other species characteristics modulated species occupancy along a gradient of hydrological change.

(A) Discussion

(B) Hydrological modification the most likely driver of invasion

Our findings suggest that, of the four hypotheses examined, an altered hydrological regime (H1) is the most likely explanation for the observed increase in invasion level – and the distinct responses of exotic and native terrestrial species – along a gradient of flow regulation impacts. The increase in proportional exotic species cover (Test 1) and decline in native species occupancy with hydrological change (Test 3) are consistent with H1. Further, despite using multiple lines of evidence, there was no evidence to suggest that the competing hypotheses accounted for the observed trends.

Exotic cover increased in drier wetlands providing support for H4 (drying), but effects of hydrological change were independent of wetland drying, at least in part, as differences in species responses to depth and hydrological changes illustrate (Test 3). Based on our results, invasion did not appear to be driven by human-elevated propagule pressure (H2) or a superior adaptation of exotic species to episodic disturbance (H3; Table 2). In line with predictions of Moles *et al.* (2012), it seems most likely that changes in disturbance regimes (i.e. flooding regimes), rather than disturbance per se, drives invasion in this system.

As proposed by Catford *et al.* (2011), modification of the disturbance regime may indirectly facilitate invasion by a) reducing the abundance of, and competition from, native species or b) directly by providing hydrological conditions to which exotic species are well adapted. Our results are consistent with the first of these two explanations because native species occupancy declined with increasing hydrological change and there was no evidence that exotic species were specifically adapted to the altered hydrological conditions (i.e. no marked increase or decrease in exotic species occupancy with hydrological change as indicated by a neutral intercept in Fig. 4). Though we lack conclusive evidence, we therefore consider it more likely that the increase in proportional exotic cover was a consequence of a decline in the occupancy and cover of native species that are adapted to the historical hydrological regime. The associated reduction in resource uptake and competition from native species may have enabled an increase in the abundance of exotic species (Davis *et al.* 2000) that are more tolerant of varied hydrological conditions. In this sense, exotic invasion in the study wetlands is likely a symptom of environmental change, rather than the driver of it (MacDougall and Turkington 2005). This points to the potential for managing exotic invasion by increasing the abundance of, and competition from, native species.

(B) Wetland drying as a secondary facilitator of invasion

Invasion in these wetlands was likely exacerbated by wetland drying, as shown by Test 1. However, findings related to species occupancy and species characteristics did not indicate why. Given that similar droughts are predicted to become more common in the future (CSIRO 2008), the reasons for the increase in exotic species abundance in drier wetlands is worth investigating, especially as such trends are not restricted to

Australia (Kominoski *et al.* 2013). Potential explanations include the increased introduction and use of drought-tolerant species in horticulture (Bradley *et al.* 2012) and pasture (D.A. Driscoll *et al.* in review) and the tendency for exotic species to have greater phenotypic plasticity and broader environmental ranges (Walther *et al.* 2009; see references in Catford *et al.* 2013).

(B) Lack of evidence for exotic colonisation ability, episodic disturbance and human association in facilitating invasion

Catford *et al.* (2011) postulated that the observed relationship between exotic terrestrial species cover and flow regulation reflected human-elevated propagule pressure and Lunt *et al.* (2012) attributed it to the higher colonisation ability of exotic species as a group. Despite drawing on a range of evidence, we found little, if any, support for either of these two explanations in our study. In addition to the lack of association between exotic cover and proximity to town, flood frequency and cattle pugging, species' responses to hydrological change – based on species characteristics – suggest that exotic species occupancy was not a function of human association (H2) nor exotics' superior colonisation ability (H3).

Given the naturally high levels of flood disturbance in riparian zones, it is explicable that exotic invasion was unrelated to flood frequency (livestock grazing may have been a different case, as discussed below). Native riparian species would be good colonisers well adapted to fluctuations in resource availability (Davis *et al.* 2000; Richardson *et al.* 2007), so adaptations and responses to flood disturbance would be unlikely to favour exotic over native species, at least under the conditions observed here.

Rather than the dominance of annuals in the exotic species pool reflecting an advantage of an annual life history under hydrological modification, as suggested by Lunt *et al.* (2012), it may reflect a bias in the types of exotic species introduced (Colautti *et al.* 2006; Chrobock *et al.* 2011) and the fact that exotic species fare better under hydrological modification than native species for reasons independent of the species characteristics examined here. As in other countries (Dehnen-Schmutz 2011), the vast majority of the 28,000 exotic plant species in Australia were introduced for pasture, horticulture or as ornamentals (Randall 2007). These species are not a random sample of the entire exotic species pool but are intentionally selected for characteristics such as fast growth rates, ease of propagation, faster germination and higher seed viability (Dehnen-Schmutz *et al.* 2007; Marco *et al.* 2010; Chrobock *et al.* 2011). This tendency to select species with certain characteristics seems to correspond with trends in species longevity and SLA found in this and other studies (Table S7; Kyle and Leishman 2009; Ordonez *et al.* 2010). As such, the higher SLA, greater seed mass and shorter longevity of the exotic species group observed in this study may simply be an artefact of introduction bias.

Unlike flood disturbance, ungulate grazing is a novel form of disturbance in Australia (Australia has no native ungulates), so it is likely that native species would be less well adapted to it than exotic species (Dorrough and Scroggie 2008). Given the long history of cattle grazing along the River Murray, native species very sensitive to ungulate grazing may already be locally extinct (Lunt *et al.* 2012). This may explain the weak relationship between exotic cover and cattle grazing in this and other studies (Jansen and Robertson 2001; Lunt *et al.* 2012).

(B) Unexplained variance at the wetland-scale

Despite including variables that represent leading explanations for riparian plant invasion, a high proportion of variation at the site-scale was unaccounted for (Fig. 1). Other analyses indicate that this is unlikely to be the result of wetland-scale differences in soil texture, pH and nutrient status, water chemistry (turbidity, dissolved oxygen, temperature, salinity), groundwater connection, tree cover, length and width of primary flow path, agricultural runoff, bathymetric variability and hydraulic connectivity among wetlands (Catford 2008; Catford and Downes 2010), though we had insufficient degrees of freedom to test for effects of all of these in combination. Other factors that might explain site-scale variation in exotic cover include undocumented human visitation (e.g. informal camping and fishing sites), floodplain land use history (e.g. logging) and disturbance from an invasive, bottom-feeding fish (*Cyprinus carpio* L., Carp).

(B) Management implications

Treating invasion as a symptom of hydrological change (MacDougall and Turkington 2005), environmental flows that reinstate crucial elements of the historical flow regime should help limit native species decline and, in doing so, should lessen exotic plant invasion (Merritt *et al.* 2010). Further research is required to identify elements of the flow regime that directly affect native flora. In the absence of information about mechanistic relationships, it appears that reinstating the frequency of mid-range flow events that occurred every 10-20 years under pre-regulation conditions would be a sound management approach in River Murray wetlands (Catford *et al.* 2011), at least under the conditions observed during this survey. These higher magnitude flows may affect flora directly, but also indirectly through correlations with other aspects of the flow regime. Given increasing water scarcity (CSIRO 2008; Capon *et al.* 2013), investment in complementary management approaches rather than solely relying on water regime management would be pragmatic.

In a time of global environmental change, it seems inevitable that the structure and composition of some ecosystems will shift (Hobbs *et al.* 2009), including riparian zones (Catford *et al.* 2013). Rather than allowing communities to self-assemble following hydrological modification and drought, managers could augment the propagule supply of native species that possess characteristics suitable under the new environmental conditions (Funk *et al.* 2008). Further research that identifies the characteristics that influence plant species' responses to altered hydrological regimes and wetland drying would be very instructive.

The approach we have used to assess potential drivers of riparian invasion is applicable to complex landscape-scale environmental problems that occur over long time frames and are poorly suited to experimental testing because of ethics and logistics. Climate change, atmospheric nitrogen deposition, estuarine and coastal dredging, noise pollution, altered fire regimes, for instance, all encompass a broad range of direct and indirect environmental changes, which typically co-occur with other environmental perturbations. Selecting species characteristics that are demonstrably and, ideally, causally linked to the confounded environmental changes in question would help to disentangle their relative effects. Like the selection of any ecological indicator, it is important to select species characteristics that are ecological meaningful, reliable, measureable, integrative and non-redundant, and are interpretable and unambiguous (i.e. avoid characteristics that may be confounded; Catford *et al.* 2012). Although the use of species characteristics to increase inference from species-environment relationships is still necessarily correlative in nature, incorporating mechanistic elements through species characteristics and using multiple lines of evidence allows a comprehensive assessment of the processes likely to drive ecological phenomena, like biological invasions.

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(A) Supporting Information

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

Appendix S1 *Additional information about the environmental and geographic characteristics of the study wetlands and study region.*

Appendix S2 *Additional information about flow regulation and the hydrology of the River Murray in the study region.*

Appendix S3 *Additional information about the drought that occurred throughout the study period.*

Appendix S4 *Description of weed classification procedure.*

Appendix S5 *Description of statistical analyses (variance components, traits analysis and trait distributions) and associated R code.*

Figure S1 *Map of the 24 study wetlands.*

Figure S2 *Partial dependency of seven traits on the effect sizes of water depth and hydrological change for native and exotic terrestrial plant species.*

Table S1 *Correlations among environmental variables for 24 wetlands and 576 quadrats, including the relative distance downstream of the study wetlands.*

Table S2 *Summary statistics of the proportional cover of total vegetation and terrestrial vegetation in the study wetlands made up of exotic species.*

Table S3 *Details of plant taxa used in the analyses showing their family, growth form, origin, longevity, germination niche, whether they are a weed of agriculture or disturbed areas and whether they are used in cultivation or as an ornamental.*

Table S4 *Correlations among the values of eight traits of the native species group.*

Table S5 *Correlations among the values of eight traits of the exotic species group.*

Table S6 *Correlations among the values of eight traits of all 76 species used in analysis.*

Table S7 *Characteristics of native and exotic species.*

Table S8 *Ways in which the seven traits examined modulate species occupancy along gradients of increasing water depth and hydrological change, as shown in Figs 4 and S2.*

Table S9 *Expected differences of species origin (exotic/native) on the effects of water depth and hydrological change on species occupancy and how traits modulate those responses, as shown in Fig. 4.*

Biosketch

Jane Catford is a Research Fellow and plant ecologist interested in biological invasions and community assembly. She is a member of three research groups: http://qaeco.com (with P.A.V and W.K.M), http://www.cbs.umn.edu/lab/tilman and http://fennerschool.anu.edu.au. Author contributions: J.A.C., B.J.D. and P.A.V. conceived the ideas; J.A.C. and C.J.G. did the hydrological modeling; J.A.C. collected the data; W.K.M. analysed the data; J.A.C. led the writing.

Table 1: Four hypotheses to explain the disproportional increase in cover of terrestrial exotic species with increasing impacts of flow regulation. Environmental gradients associated with Hypotheses 2, 3 and 4 may be confounded with hydrological change, so H2, H3 and H4 may be fully or partially responsible for the observed relationship with flow regulation impacts. Tests 1, 2, & 3 refer to the analyses as described in the Methods. #If the competing hypotheses are true, we would expect all environmental gradients associated with H2, H3 and H4 to be correlated with hydrological change [i.e. this would then explain the observed relationship between exotic cover and hydrological modification observed by Catford *et al.* (2011)]. *All trends refer to increasing impacts of flow regulation, though we also examine the same trends in relation to other important environmental gradients; hypothesised trend refers to both native and exotic species unless otherwise stated.

Hypothesis	Description	Test 1: Variation in exotic cover#	Test 2: Species characteristics	Test 3: Species occupancy along environmental gradients*
1. Hydrological change	Flow regulation facilitates invasion because: a) abundance of native species adapted to the historical hydrological	Higher exotic cover with greater hydrological change.	No test.	Occupancy of native species will a) decline or b) be unaffected.

	regime declines, allowing species with a broader environmental range to increase; and/or b) exotic species are specifically adapted to the altered hydrological conditions.			Occupancy of exotic species will a) be unaffected or b) increase.
2. Human-elevated propagule pressure	Exotics have a storage and dispersal advantage over native species because of their strong association with humans. Their higher propagule availability is particularly advantageous under high resource availability.	Higher exotic cover close to human activities.	Greater proportion of exotic species pool is used in cultivation or classified as a weed.	Higher occupancy of cultivated species and weeds of agriculture and disturbed areas.
3. Superior colonisation ability	Short-term increases in resource availability from episodic disturbance favours species with high colonisation	Higher exotic cover with more frequent flooding.	Exotic species pool biased towards annuals, shorter	Higher occupancy of shorter species and those with higher SLA, lower

	ability and rapid growth. High colonisation ability may also favour terrestrial species following flood cessation.	Higher exotic cover with more cattle pugging.	species and species with higher SLA and lower seed mass.	seed mass and an annual life history.
4. Wetland drying	Exotics are better adapted to drier conditions than natives and the main effect of flow regulation is drying. Drought may compound effects of drying from flow regulation.	Higher exotic cover with lower soil moisture and at shallower water depths.	Exotic species pool biased towards dry germinants, perennials and species with larger seeds.	Higher occupancy of dry germinants, perennials and species with larger seeds.

Table 2: Findings relating to four hypotheses to explain trends in exotic plant invasion in River Murray wetlands. Refer to Table 1 for details. findings support hypothesis; ~ findings provide partial support for hypothesis (i.e. some, but not all findings support hypothesis); **0** findings indicate mixed (i.e. findings are contradictory: some support, some refute) or no support for hypothesis.

Hypothesis	Test 1: Variation in exotic cover	Test 2: Species characteristics	Test 3: Species occupancy along environmental gradients
1. Hydrological change	*Support* Increases with greater hydrological change.	No test	*Support* Occupancy of native species declines with greater hydrological change, but exotic species occupancy is unaffected.
2. Human-elevated propagule	**0** *No support* Unrelated to proximity to town despite positive correlation between	~ *Partial support* Greater proportion of exotics classified as a weed,	**0** *No support* Occupancy of weeds and cultivated species does not increase with

pressure	hydrological change and distance to town.	but similar proportion of exotics and natives used in cultivation.	greater hydrological change or wetland drying.
3. Superior colonisation ability	**0** *No support* Unrelated to flood frequency and cattle pugging despite positive correlation between hydrological change and flood frequency (no correlation with cattle pugging).	**0** *Mixed findings* Exotics have higher SLA and shorter lifespans, but do not have smaller seed mass and are similar in height.	**0** *No support* Occupancy of shorter species, annuals and species with higher SLA, lower seed mass does not increase with greater hydrological change or wetland drying.
4. Wetland drying	*Support* Increases with less standing water and possibly with lower soil moisture despite lack of correlation between hydrological change and soil moisture	**0** *Mixed findings* Greater proportions of exotics have larger seeds and are dry germinants, but	**0** *No support* Occupancy of dry germinants, perennials and species with larger seeds does not increase with greater hydrological change or wetland

	and water depth.	most are not perennial.	drying.

Figure captions

Figure 1: Variance components for a model of the proportion of terrestrial cover that is exotic (logit-transformed) plotted on the standard deviation scale. We consider relationships important if the environmental variables account for at least 0.5 SD of the proportional exotic cover and the 95% credible intervals do not overlap zero. Black dots show the medians of the posterior densities with thick lines showing one posterior standard deviation either side (68% credible intervals) and thin lines indicating two posterior standard deviations (or 95% credible intervals).

Figure 2: Partial dependence plots from the model of the proportion of terrestrial cover that is exotic (Fig. 1). Lines indicate line of best fit and shading shows the 95% credible intervals. We consider trends significant if the 95% credible intervals do not overlap zero.

Figure 3: Comparison of modeled distribution of logged values of a) specific leaf area, b) plant height and c) seed mass for native (black) and exotic (grey) plants. Distributions illustrate how functional characteristics differ between native and exotic species groups. Rug plots show observed average trait values of individual species.

Figure 4: The contributions of traits to species occupancy relative to water depth (left panels) and hydrological change (right panels). The uppermost panels show how the occupancy of native and exotics terrestrial wetland species varies with water depth and hydrological change (main effects). A positive effect size indicates an increase in species occupancy along that environmental gradient. Coefficients in the other panels indicate how traits modulate species occupancy relative to these environmental variables while other traits and environmental variables are held at their means. A positive effect size indicates that higher values of that trait increase the probability of species occupancy

along that environmental gradient. We consider effects significant if the effect sizes are at least ±0.5 SD and the 95% credible intervals do not overlap zero (marked with an asterisk). Origin (exotic/native) only had a distinct effect on species' responses to hydrological change (i.e. the 95% credible intervals of differences in parameter estimates for the native and exotic groups overlapped zero for all effects except hydrological change; Table S9). Filled symbols native, open symbols exotic. Bars represent two posterior standard deviations (or 95% credible intervals) around parameter estimates. Vertical grey lines mark ±0.5 SD. WD, water depth; HC, hydrological change. Numbers provided in Table S8.

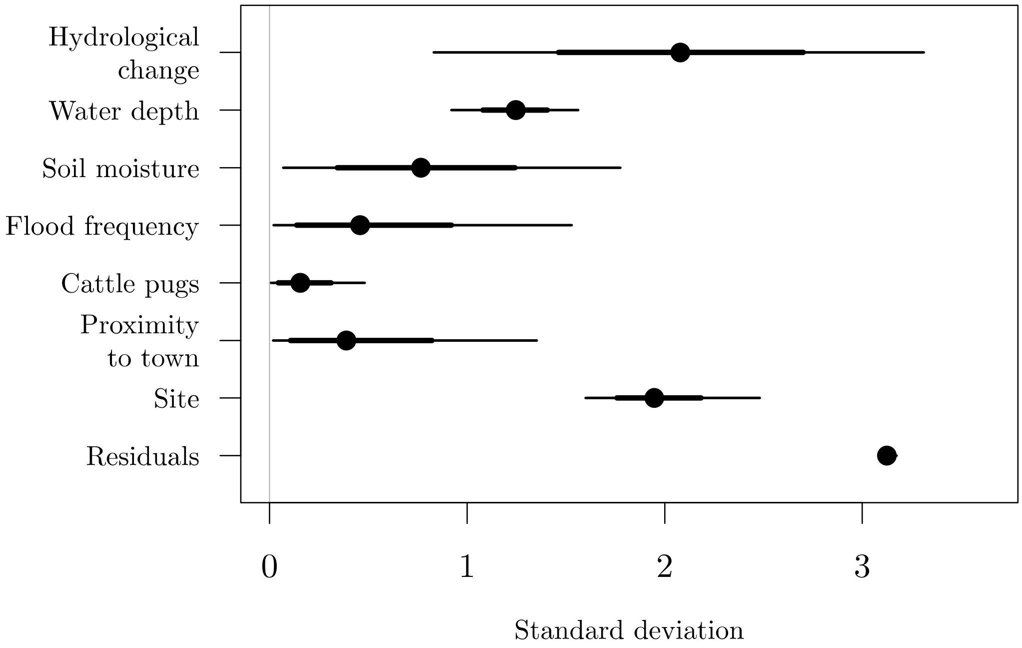

Hydrological change
Water depth
Soil moisture
Flood frequency
Cattle pugs
Proximity to town
Site
Residuals
0
1
2
3
Standard deviation

Fig. 1

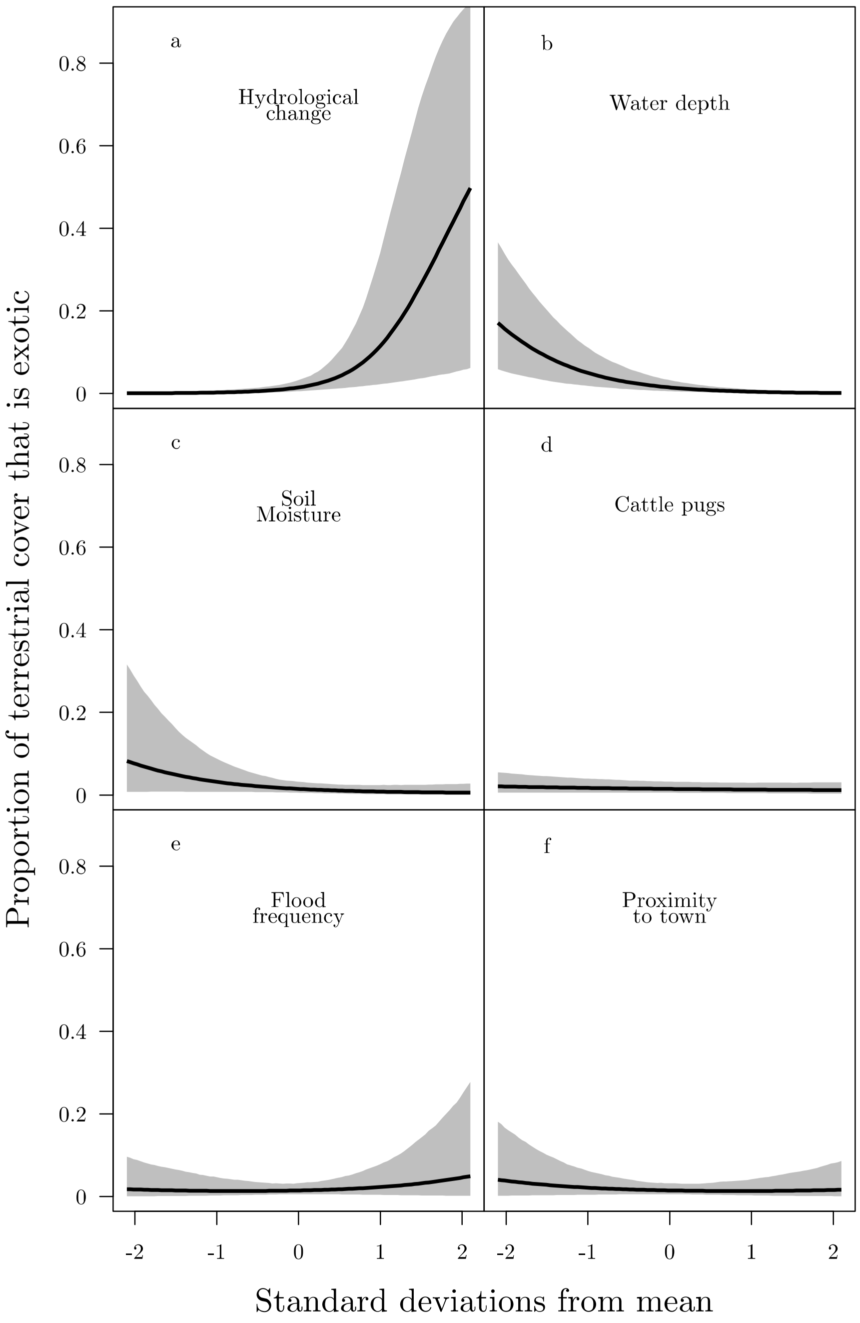
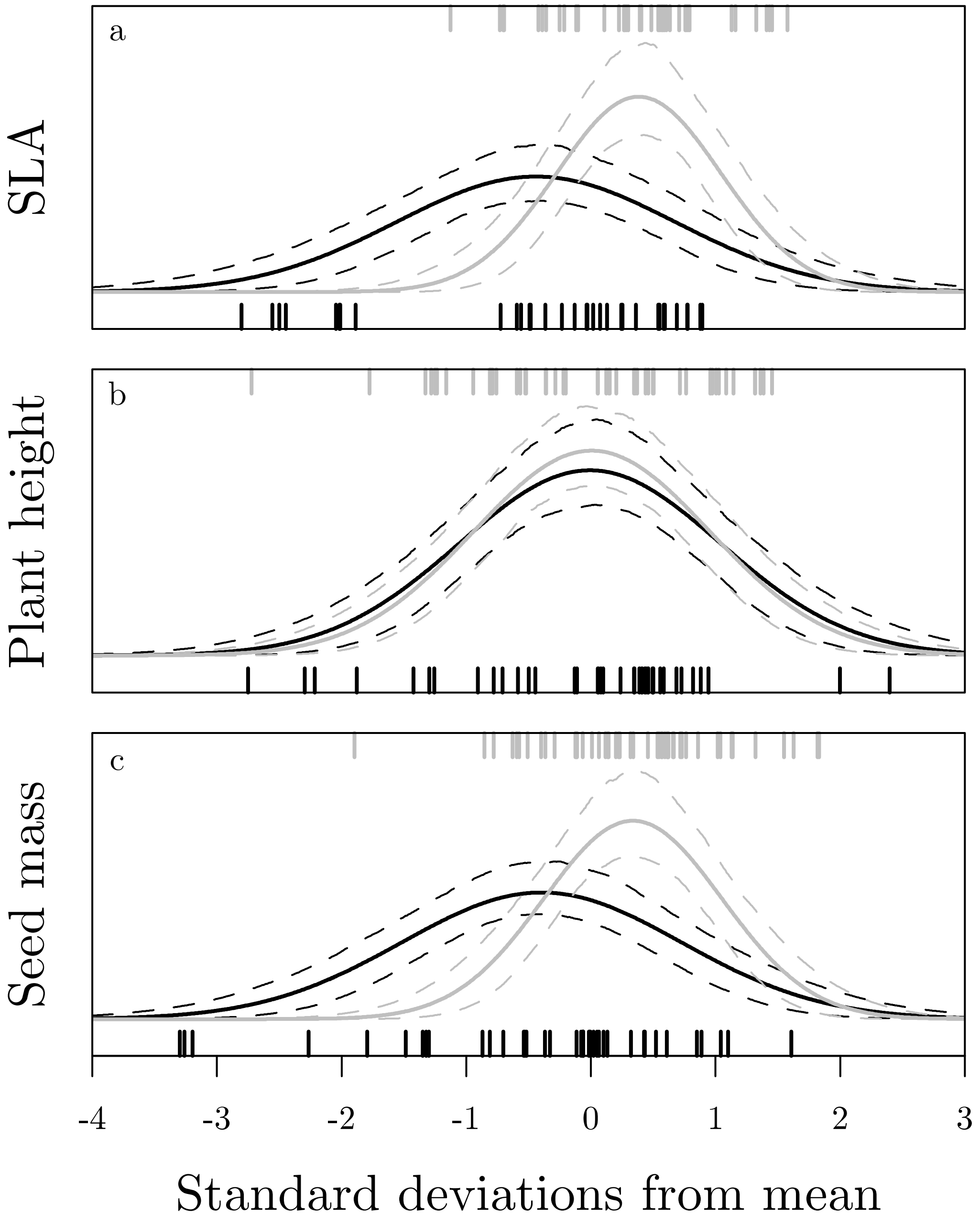

a
Hydrological change
b
Water depth
c
Soil Moisture
d
Cattle pugs
e
Flood frequency
f
Proximity to town
0.8
0.6
0.4
0.2
0
-2
-1
0
1
2
Proportion of terrestrial cover that is exotic
Standard deviations from mean

Fig. 2



a
SLA
b
Plant height
c
Seed mass
-4
-3
-2
-1
0
1
2
3
Standard deviations from mean

Fig. 3

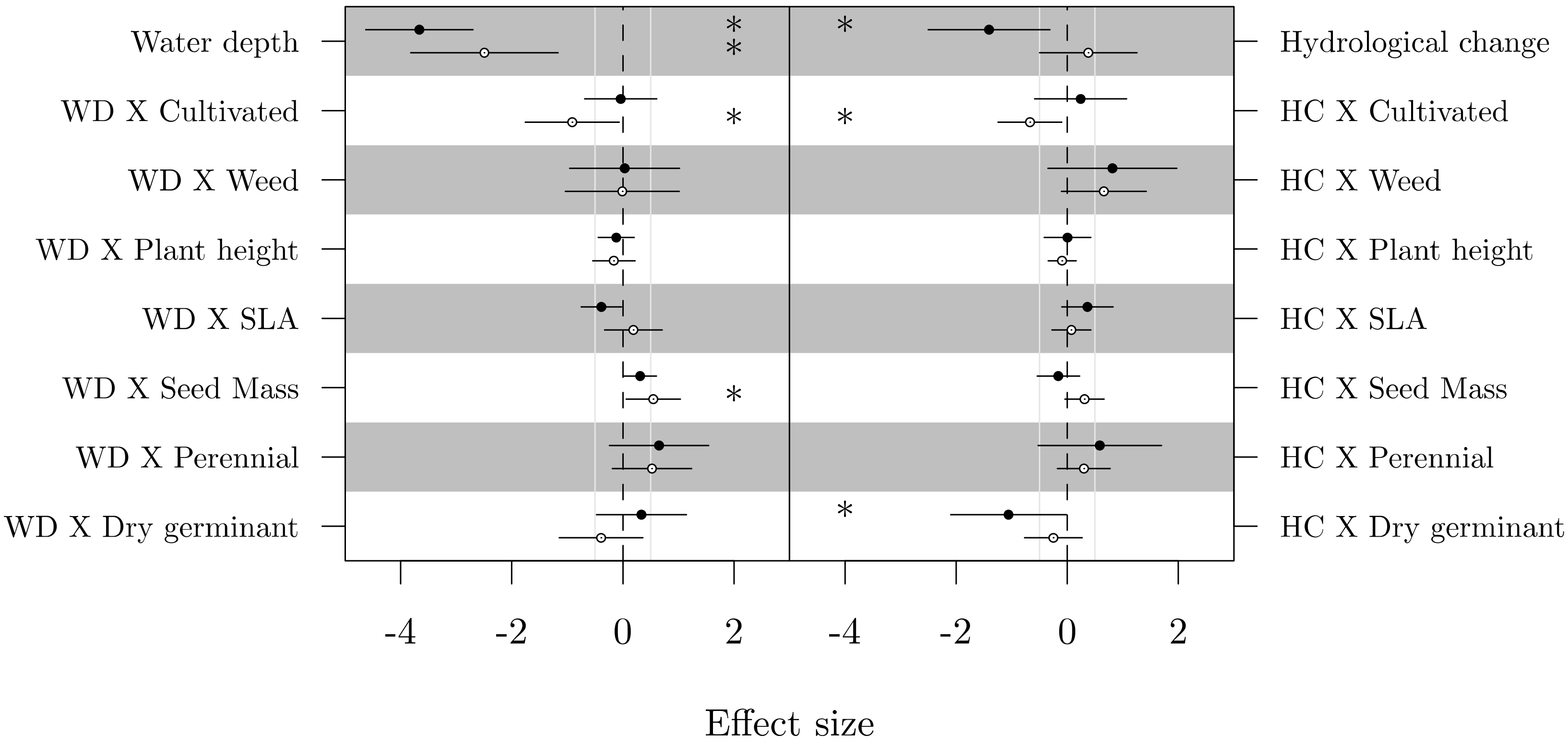

Water depth
WD X Cultivated
WD X Weed
WD X Plant height
WD X SLA
WD X Seed Mass
WD X Perennial
WD X Dry germinant
Hydrological change
HC X Cultivated
HC X Weed
HC X Plant height
HC X SLA
HC X Seed Mass
HC X Perennial
HC X Dry germinant
*
*
*
*
*
*
*
-4
-2
0
2
-4
-2
0
2
Effect size

Fig. 4