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Plant traits of propagule banks and standing vegetation reveal flooding alleviates impacts of agriculture on wetland restoration

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Running Title: Plant traits show flooding restores wetlands

Summary

1. Restoration of degraded plant communities requires understanding of community assembly processes. Human land use can influence plant community assembly by altering environmental conditions and species' dispersal patterns. Flooding, including from environmental flows, may counteract land use effects on wetland vegetation. We examined the influence of land use history and flood frequency on the functional composition of wetland plant communities along a regulated river.
2. We applied fourth corner modelling to determine species' trait-based responses to flooding and land use by combining data on i) the occupancy and abundance of species in propagule banks and standing vegetation, ii) species traits, and iii) environmental conditions of 22 standing vegetation and 108 soil propagule bank study sites. We used analysis of deviance to test how well each dataset characterised trait–environment interactions, and generalised linear models to identify traits related to species' responses.
3. The occupancy and abundance of native species in the propagule bank and standing vegetation increased with flood frequency and decreased with duration of

agricultural land use. Species in standing vegetation with water-borne propagule dispersal (hydrochory) showed similar trends. In contrast, species with higher specific leaf area were associated with longer land use duration.

4. Identifying trait–based differences in the propagule bank and standing vegetation can help disentangle effects of dispersal and environmental filters. The occupancy and abundance of hydrochorous species in standing vegetation were negatively related to land use duration, but hydrochorous species were positively related to land use duration based on their abundance in the propagule bank. This suggests that land use does not limit plant dispersal, but acts as an *in situ* abiotic filter limiting species presence in standing vegetation.

5. *Synthesis and applications.* Land use duration and flood frequency have opposite effects on plant community traits in floodplain wetlands of the Macquarie Marshes, Australia. Legacies of agriculture can impede restoration of plant communities. Environmental flows that increase flooding may alleviate these impacts, especially in areas that have been used for agriculture for over 20 years, by providing dispersal and environmental filters that favour native wetland species. More flooding will likely be required to restore floodplains with longer histories of agricultural land use compared to floodplains less impacted by agriculture.

Keywords: agriculture, community assembly and reassembly, community composition, environmental flows, exotic species, flood frequency, floodplain wetland vegetation, functional traits, native species, riparian plant invasion, seedbank

1. Introduction

Identifying plant trait variation along environmental gradients offers a way of understanding community assembly and can provide insights for restoration (Keddy 1992; Keddy 1999; Weiher et al. 1998; Götzenberger et al. 2012; Fournier et al. 2015). Community assembly theory posits that a community is comprised of species that can i) disperse to the site in question (either currently or historically), ii) tolerate its environmental conditions, and iii) co-occur with other biota at that site (e.g. by withstanding competition and predation; Belyea & Lancaster 1999). Consistent with these three conditions, the process of community assembly is often characterised as a series of three filters [i.e. i) dispersal filter, ii) abiotic filter and iii) biotic filter], which exclude species that lack traits required to pass through the filters (Fig. 1; Keddy 1992; van der Valk et al. 1992; Belyea & Lancaster 1999; Götzenberger et al. 2012; Catford & Jansson 2014). Plant traits and the functional composition of a community can help reveal the relative importance of the dispersal, abiotic and biotic filters, and mechanisms that underpin these (Catford & Jansson 2014).

Functional characteristics of standing vegetation, assessed by combining information on plant species' functional traits with species' occupancy or abundance data indicate the functional composition of the actual species pool (*sensu* Belyea & Lancaster 1999; Fig. 1). In contrast, propagule banks are a subset of the geographic species pool under the dispersal filter because they do not include short-lived propagules (Fig. 1; Chesson 2003). Dormancy within propagule banks enables dispersal-through-time (Baskin & Baskin 1998, Brock et al. 2003, Chesson 2003, Middleton 2003). At a given site, species present in standing vegetation have passed through dispersal, abiotic and biotic filters, whereas species present in the propagule bank have passed through the dispersal filter, but may or may not germinate and establish in prevailing abiotic and biotic conditions. The traits represented within these different species pools provide insights into the relative effects of these different filters on community assembly, even though species traits may vary with life stage (Lohier et al. 2014).

Landscape-scale restoration strategies typically involve manipulating dispersal and abiotic filters to preferentially select species, and thus communities, with desirable functional traits (Brudvig 2011, Catford & Jansson 2014). Effects of dispersal and abiotic filters can be hard to disentangle as both lead to trait convergence, where traits of co-occurring species are more similar than expected by chance, and both filters operate at similar spatial scales (e.g. landscape; Fig 1; Götzenberger et al. 2012; Catford & Jansson 2014). However, it is crucial to know whether dispersal or environmental conditions are limiting restoration success as remedial management actions for each condition differ (Catford & Jansson 2014).

Humans have directly or indirectly altered the composition of wetland plant communities across the world through activities that alter wetland flood regimes, such as impounding, extracting upstream water, wetland draining and farming. Wetlands are one of the most threatened and degraded types of ecosystems worldwide, and hence many are targets for restoration (Kingsford, 2000; Toth & van der Valk, 2012). In many southeastern Australian wetlands, upstream dams and water extraction have disrupted historical flood regimes, which maintained biodiversity and ecosystem services (Kingsford, 2000). Within wetlands along regulated rivers, two key processes influence restoration outcomes: land degradation (from farming) and flood regime alteration (from river regulation; Fig. 1; Kingsford, 2000; Campbell et al. 2014; Dawson et al. 2016). Both processes are mediated by humans and represent landscape-scale environmental gradients. Flood gradients drive wetland vegetation composition and community assembly, typically resulting in plant trait convergence (Weiher et al. 1998; Keddy 1999; Campbell et al. 2014). Wetland restoration through re-introduction of historical flood regimes is increasingly used to accelerate restoration processes by manipulating effects of this filter (Toth & van der Valk 2012; Catford & Jansson 2014; Moreno-Mateos et al. 2015). Flood re-instatement can change the functional composition of vegetation towards communities that are desired by managers, i.e. communities made up of native species that occurred at the site historically (referred to as ‘desired species’; van Bodegom et al. 2006). Success, however, may be limited, largely because of the dominance of ‘undesired’ ruderal or exotic species or because of historical legacies (Suding et al. 2004; Toth & van der Valk 2012), which may be crucial in determining restoration outcomes (Brudvig & Damschen 2011; Brudvig 2011).

We sought to disentangle effects of dispersal and abiotic/biotic filtering in a floodplain wetland undergoing restoration, potentially under the influence of land use legacies. Flood regimes are being reinstated through managed environmental flows and removal of levees that disrupt floodplain connectivity. By assessing trait-based responses of plants to flooding and land use duration, we aimed to understand how human-mediated environmental gradients influence community assembly (Fig. 1). Consistent with theory (Keddy 1992; Keddy 1999; Weiher et al. 1998; Götzenberger et al. 2012; Fournier et al. 2015), we reasoned that the observed trait-based trends would provide insights into environmental conditions that constrain or facilitate restoration of wetland vegetation.

Using fourth corner modeling (Brown et al. 2014) and six plant traits that are likely to be important for arrival, establishment and persistence in wetlands, we asked:

> How does the functional composition of the geographic species pool (indicated by species abundance in the propagule bank) and the actual species pool (indicated by species occupancy and abundance in standing vegetation) change along flood frequency and land use gradients?

The six plant traits are important and commonly used in wetland studies (McGill et al. 2006). Details of each trait, reason for selection, and the hypothesized relationship between each trait and environmental gradient are in Table 1. We expected that the abundance of species that are native, woody and long-lived would be positively related to flood frequency and negatively related to land use intensity, and that species with high SLA and heavy seeds would increase along both environmental gradients.

2. Materials and methods

2.1 Study Site

Our study sites were located within the Pillicawarrina property, a private leasehold in middle of the Macquarie Marshes. The Macquarie Marshes is a Ramsar-listed wetland in south-eastern Australia with iconic wetland vegetation and large colonial waterbird breeding sites (Thomas et al. 2010). Fed by the regulated Macquarie River, the Macquarie Marshes suffer from declines in flooding magnitude, duration and variability due to upstream extraction for irrigation, negatively impacting floodplain vegetation and other biota (Kingsford 2000, Thomas et al. 2011). Only about 10% of the Macquarie Marshes is in protected areas, with the remainder on privately owned (or leased) land, which is mostly grazed with some cultivation.

Pillicawarrina was first cultivated in the 1980s for wheat (dryland) and cotton (irrigated) agriculture, replacing largely intact floodplain vegetation consisting of *Eucalyptus camaldulensis* (river red gum) forests, *Duma florulenta* (lignum) swamplands and associated marsh understory communities (Paijmans 1981). The 12 fields in the Pillicawarrina study area were either cultivated for varying periods (1-23 years (continuous)), or cleared but never cultivated (see Appendix 1 & 2; Dawson et al. 2017a & b). Levee banks were also built to protect most of the area from flooding, however large floods still inundated the whole area periodically.

In 2008, Pillicawarrina's water license and 2,346 hectares of land were purchased under a government program to restore historical vegetation communities (DECCW NSW 2011). Assisted natural restoration was initiated in 2009; levees were breached at strategic points and culverts improved to enhance river-floodplain connectivity (DECCW NSW, 2011). The area was flooded by natural floods supplemented with environmental flows in 2009/10, 2010/11 and 2011/12. The natural floods marked the end of a decade long drought in the Macquarie Marshes. It is difficult to quantify exact hydroperiods for different parts of Pillicawarrina because the whole property is very flat (1 m fall over 2.4 km, Appendix 1). However, we were able to gain flood frequency from satellite information (Thomas et al. 2011). More details of the study site and its history can be found in Appendix 1.

2.2 Human mediated environmental gradients

The two environmental gradients we studied were the duration of land use in years (clearing or cultivation) and the number of floods over the past 25 years (from a total of 32 flood events in the Marshes; includes all events for which data are available over the 25 year period). These environmental gradients were selected because historic land use can structure reassembling communities (Brudvig 2011) and flooding is known to drive plant community assembly in wetlands (Weiher et al. 1998; Keddy 1999).

Land use duration was derived from interviews with the Pillicawarrina property manager. Cultivation involved wheat crops, which were grown with chemicals. We defined land use duration as the number of years a field was cleared or cultivated. We did not consider grazing because the whole area of the Macquarie Marshes, a portion of which is included in the

Pillicawarrina property, have been grazed for 150 years, so we expected grazing impacts to be similar across the 12 study fields (there are no records of grazing duration or densities for Pillicawarrina). Cattle and feral pigs have continued to graze the area, but again, no records are available to evaluate the effect of grazing.

Flood frequency was estimated from flooding extent maps for every flood event from 1988 to mid-2012 (32 events over 25 years; Thomas et al. 2011, Thomas et al. unpublished data). A site was considered inundated when mapped as flooded from satellite imagery taken at any point during an event. Standing vegetation surveys were undertaken between 2011-13 and the propagule bank was sampled in 2014. Strong Pearson correlations between the flooding frequency used in our models and flooding frequency prior to and after surveys mean model results would be extremely similar (prior: occupancy dataset r=0.99, abundance dataset r=0.96, after: occupancy dataset r=0.99, abundance dataset r=0.99). A similarly strong correlation exists between the flooding frequency used in the models and after propagule bank sampling (r=0.99).

A third variable, time since last land use event, was excluded from analyses as it was strongly correlated with land use duration across all three datasets (propagule bank dataset: r= 0.9, standing occupancy dataset r=0.9, standing abundance dataset r= 0.8; Appendix 3). Time since last land use event was also negatively correlated with flood frequency (propagule bank dataset: r= -.6, standing occupancy dataset r=-0.6, standing abundance dataset r= -0.3). As correlations between land use duration and flood frequency (Appendix 3) were below predicted distortion levels for models (r=0.7), we used both of these variables in our models (Dormann et al. 2012).

2.3 Vegetation data

Surveys of standing vegetation

We collected plant occupancy data from 22 sites across seven fields and plant abundance data from 14 sites across six of the 12 fields (a subset was used due to accessibility issues during flooding; Dawson et al. 2017a). Woody species were surveyed within 20 m x 20 m plots, and within these plots, herbaceous species were surveyed from five randomly placed 1 m x 1 m quadrats. Occupancy data were sourced from two surveys of standing vegetation (Berney 2012 (Survey A), Dawson et al. 2017a (Survey B); Appendix 1) to characterise as much of the area as possible.

We quantified occupancy by recording a species as present if it was observed during any one of the three visits from either survey (Survey A: March 2011, March 2012 and April 2013, Survey B: November 2012, January and March 2013). Abundance was quantified in Survey B by counting the total number of woody species or, for herbaceous species, using a modified point-intercept method (Dawson et al. 2017a). This method used a 1 m * 1 m grid of 25 pins where species abundance is estimated based on the number of times a pin touches a given species. As this survey consisted of three visits across the flood cycle, numbers of shrubs and trees (RBGDT 2015) were averaged across sampling times to avoid recounts. Given that herbaceous vegetation rapidly changed in composition among visits and different parts of the plot, we took the peak abundance (e.g. the highest count of any survey) for each species (following Fargione & Tilman 2005). We also had two control sites in Survey B, with vegetation that had no history of clearing or cropping, within 200 m of the study area.

Propagule bank surveys

We used a greenhouse emergence assay of the soil propagule banks to identify the traits of plants present in the propagule banks (Galatowitsch & van der Valk 1996; Brock et al. 2003; Middleton 2003). We collected soil at nine sites within each of the 12 fields (108 total), across a floodplain elevation gradient (see Dawson et al. 2017b). The floodplain elevation gradient was identified using a high resolution digital elevation model with sites located either i) within, ii) adjacent to, or iii) 50-100 m from small (<20 cm depth) floodplain channels (Appendix 1). Locations of the soil collection and standing vegetation within each strata and field were independent (Appendix 1). Soils were collected from 10 randomly placed cores within each plot (cores: 5 cm diameter and 5 cm depth, i.e. 0.3925 L of soil), which were combined in the same bag, air-dried and stored prior to germination. Additional samples of soil were tested for residual herbicides, but no traces of herbicide were found (Dawson et al. 2017b).

The propagule bank samples were subjected to three flooding treatments (inundated, saturated and damp combinations) over a period of 12 weeks in a greenhouse, kept at spring temperature (20-27 ^{0}C) for the Macquarie Marshes. We counted the number of germinants that emerged and identified them to species, where possible. Woody species were not expected to germinate, as these species rarely occur in the soil propagule banks of floodplain wetlands in Australia (Chong & Walker 2005; Dawson et al. 2017b). Seeds and propagules of woody species found in the Macquarie Marshes are short-lived, and usually lie on the soil surface and germinate shortly after dispersal (e.g., within 2 weeks for *Duma florulenta*; Chong & Walker 2005).

2.4 Trait data

We used six plant traits (Table 1) shown to be important for wetland processes (McGill et al. 2006) and easily measurable across a large number of species (Table 1). We included specific leaf area (SLA) because it can indicate plant competitiveness, growth rate, successional context in restoration areas and is often used in wetlands (Table 1), allowing comparison of our results with other studies. As such, we expected SLA with to be positively related to flooding frequency (due to higher competition and growth rate in these areas) and land use duration (early succession; Table 1).

We sourced trait information from field measurements, the literature (28 references; listed in Appendix 4) and expert opinion. Traits were collected for 78 taxa, generally single species but occasionally several species, representing >90% of abundance/occupancy for each dataset (Appendix 5). We considered using three additional traits (clonality, need for flood during lifecycle and ability to survive one week of flood), but they were strongly correlated with other selected traits, so we excluded them from analyses (Appendix 3). Plant height was not used because wetland species can have decumbent, floating and/or plastic growth, making interpretation difficult (Catford & Jansson 2014).

We used the Kew Seed Information Database (RBG Kew 2015) or field sampling to source seed masses (Appendix 5). For species with no seed mass data in either literature or sampling (18 species or genus groups), an estimate was derived by averaging values for at least five congeners (Appendix 5). Four exceptions were made where species had limited information: *Lemna* sp., *Pratia concolor*, *Azolla* sp. and *Ricciocarpus nutans*. The first two had only one congener (*Lemna perpusilla* and *Pratia hederacea*), for which seeds were morphologically similar to study species, so we used their seed masses as surrogates. While the second two have very small diaspores (*Ricciocarpus nutans* is smaller than *Azolla* sp.; Appendix 5), for which we were unable to find mass data. We used the number of spores per gram of sediment that were available for *Azolla arctica* (Appendix 5) and divided this by one gram as a conservative estimate of mass (3.083E-6 gm) for both *Azolla* sp. and *Ricciocarpus nutans*.

We sampled plants for SLA and seed mass in November 2013 from at least five healthy individuals within Pillicawarrina or nearby (following Pérez-Harguindeguy et al. 2013). SLA values were sourced from the literature for species that were not found during this sampling. Estimates for most species were from either Catford et al. (2014) or Ordonez & Olff (2013), both Australian-based studies conducted in similar wetlands. However, for 12 species (or genus groups), no species measurements could be found and mean SLA values of a minimum of four congeners (average of six) were used. Congeners for six taxa were sourced from Catford et al. (2014) and Ordonez & Olff (2013), with the remainder sourced from individual studies (Appendix 4). Additionally, for a group in the propagule bank consisting of *Chenopodium cristata, C. melanocarpa* and *Dysphania pumilio* (seedlings indistinguishable from each other and mature leaves morphologically similar), we used the average SLAs of the two *Chenopodiums,* as there were no published data on *Dysphania pumilio*. Nine taxa in the data set could not be identified to species' level and so were grouped into genus or groups of similar species (e.g. *Juncus* spp.; Appendix 5).

Remaining life history traits were sourced from floras (Cunningham et al. 1992; RBGDT, 2015) or from personal observations in the field. We only included plant species' primary dispersal mode in our models. Although many plants use multiple dispersal vectors (e.g. wind dispersed seeds often float on water too), they do so in varying degrees, which made statistical analysis impractical. Primary dispersal method was sourced from floras and the detailed descriptions of species in Cunningham et al. (1992). We listed *Xanthium occidentale*, an exotic burr, as dispersing primarily through hydrochory (instead of the published zoochory) based on field observations. Although we focused on primary dispersal of species, it should be recognised that most species have secondary dispersal methods. *Juncus* species were classified as natives as there were no records of exotic *Juncus* species occurring in the area. We could not allocate flood survival for 34 species and so we surveyed 17 experts from across Australia (ability to survive one week of flood, removed from analysis due to correlations with hydrochorous dispersal). Experts were identified through professional networks and had several years' experience working with wetland plants (average of 13 years). Inconsistencies in answers were reconciled by using the answer with the highest level of agreement.

2.5 Statistical analysis

We used fourth corner modelling (Brown et al. 2014), implemented through the mvabund package in R (Wang et al. 2012; R Development Core Team 2015) to search for trait convergence across the two environmental gradients. This type of modelling has advantages over traditional multivariate methods, like distance-based ordination, as it accounts for mean-variance relationships (Warton et al. 2012). Fourth corner modelling illustrates relationships between plant traits and environmental variables by fitting a predictive model (using Generalised Linear Models; GLMs) of all species, at all sites with environmental factors, traits and species observed as explanatory variables. This enables the strength and direction trait-environment interactions to be analysed, and indicates how species' functional traits relate to species' responses to environmental gradients (Dawson et al. 2017a & b; Brown et al. 2014). Model inputs included the selected traits for each species, the environmental gradients quantified at each site, and species data for each site from each survey type. Site by species data consisted of presence/absence for the standing vegetation occupancy dataset and abundance data for the propagule bank and standing vegetation abundance datasets. Species occurring in only one or two plots were removed before analysis to improve computational stability. Environmental variables and continuous trait variables were $\log_{10}$ transformed before analysis. Multi-collinearity was explored within trait and environmental variables, using pairwise correlation plots (Zuur et al. 2010), and correlated variables excluded.

The fourth corner analysis fitted a predictive model of abundances (or occupancy) for all species (L) simultaneously, as a function of the environment by site matrix (R), the species by trait matrix (Q) and their interaction (RxQ). The RxQ interaction provided information on the variation of trait abundance (or occupancy) with environmental variables. If an environmental gradient acts as a community assembly filter resulting in trait convergence, this will be indicated by significant trends in the occurrences of species with specific traits along that environmental gradient. For example, if higher flood frequency were to favour species with higher SLA, then a positive interaction would be observed between SLA and flood frequency.

We used a reduced propagule bank dataset of two randomly selected sites from each of the 12 fields (24 sites in total) to examine the effect of a smaller sampling effort, i.e. a sampling effort that was similar to the standing vegetation surveys. A negative binomial distribution was used to account for overdispersion when modeling abundance in the standing vegetation abundance and the propagule bank, and a binomial distribution was used for the standing vegetation occupancy. No woody species emerged during the germination trials, so the woody trait was not included in propagule bank models.

To answer our question about trait-based trends along the two environmental gradients across the three vegetation datasets (propagule bank, standing vegetation occupancy and abundance), we conducted three types of analysis using fourth corner models. First, we built models, including a block function to account for nesting within fields and a resampling approach (1500 iterations) to test for significance of trait-environment relations. We do not report R^2 values from these models, as the 4th corner terms and data with many zeros constrains R^2 values. Second, to examine patterns of trait convergence, we fit models without the block function and including a LASSO approach, which set trait-environment interactions to zero where they did not explain variation in the response variable (Brown et al. 2014). LASSO approaches constrain some estimates of model parameters (effectively shrinking them to 0) through penalised likelihood (Brown et al. 2014). Standardised coefficients of trait-environment interactions from the model were then plotted to show the direction and strength of trait variation with human mediated environmental gradients.

Third, we explored responses of binary traits (e.g. annual vs perennial) to environmental variables that had interactions terms greater than 0.2 in the LASSO models (e.g. to determine if perennials increasing or annuals decreasing was driving an observed relationship with longevity). Additional models were fitted to predict abundances across one environmental gradient, while holding the other environmental gradient at a mean value (hereafter called individual trait-environment models). Standard deviations were calculated via a resampling approach using 50 iterations. These models did not include interactions with other traits.

3. Results

Generally, longer land use duration was associated with increased abundances of exotics and dryland species across datasets and the opposite was observed with increased flooding frequency. Within the propagule bank, the effects of land use were also more pronounced in less frequently flooded areas, which harboured higher abundances and diversity of exotic and ruderal species (e.g. *Rapistrum rugosum* and *Dysphania* spp.). Increased inundation partly mitigated the effect of land use history, with increased abundances of species such as *Myriophyllum papillosum*. In standing vegetation surveys, sites with increased flooding frequency had increased abundances of wetland species (e.g. *Eleocharis* spp.), while more intensive land use was associated with higher abundances of terrestrial functional groups, comprising species like *Calotis scapigera* and *Brassicaceae* spp. (see Dawson et al. 2017a & b for details on the species' abundances).

There was evidence that land use duration and flood frequency led to trait convergence in the propagule bank and standing vegetation, particularly for SLA, species provenance and dispersal mode, which displayed strong responses to both gradients (detailed below). The models for the three datasets all had significant *p*-values: soil propagule bank with 108 sites, $p = 0.001$ (propagule bank with only 24 sites was also significant, with $p = 0.005$), extant vegetation occupancy, p = 0.009 and standing vegetation abundance, p = 0.001. Standing vegetation abundance had the lowest sample numbers (14 sites only) but was the most significant out of the three models constructed.

The strongest trait-environment interaction occurred with models of standing vegetation abundance (Fig 2). SLA was positively related to land use duration, indicating that species with higher SLA were likely to increase in abundance in fields with longer agricultural history. SLA exhibited a similar relationship with land use duration in models of standing vegetation occupancy and propagule bank, although not as strong as that for standing vegetation abundance.

Across all models, native species decreased with increasing land use duration and increased with flood frequency (Fig. 2). In individual trait-environment interaction models (Fig. 3) based on propagule banks and standing vegetation abundance, native species decreased with increasing land use while exotics slightly increased (Fig. 3a, d). In contrast to land use, the abundance of native species in standing vegetation increased and the abundance of exotic species decreased with increasing flood frequency (Fig. 3e).

In the propagule bank higher abundances of species that disperse by water (hydrochores) and lower abundances of animal-dispersed plants (zoochores) were associated with higher flood frequencies. Individual models of these two interactions predicted that, while abundances of both hydrochores and non-hydrochores increased with flood frequency (though hydrochores had higher predicted abundances), non-zoochores increased with increasing flooding and zoochores strongly declined (Fig. 3b, c). Hydrochorous species in the models of standing vegetation (occupancy and abundance) showed positive relationships with flood frequency and negative relationships with land use duration (Fig. 2). Annual species increased with both increasing land use duration and flood frequency in models of the propagule bank but decreased with increasing flooding in standing vegetation abundance models (Fig. 2). Woody species decreased with land use duration in the occupancy models but not in the abundance models.

Eight of 14 trait-environment interactions predicted in Table 1 were supported, two had equivocal or mixed support, and the remaining four were not supported (Table 2). All vegetation responses to increasing land use duration had some level of support, except for increasing abundances of zoochores in the propagule bank. Predictions of decreasing hydrochores with increasing land use duration had mixed results; they were supported in standing vegetation models, but refuted in propagule bank models. Our predictions of response to increasing flood frequency were only supported in four out of seven cases. Hydrochores and natives increased with flooding (across all datasets) and zoochores and annuals declined (in the propagule bank and standing abundance datasets respectively). Predicted response of annuals to increasing flood frequency had support in the abundance dataset for standing vegetation but weak refutation in the propagule bank and occupancy of standing vegetation.

4. Discussion

Plant traits represented in species pools of both standing vegetation and soil propagule banks suggest that both flood frequency and land use duration influenced the assembly of restored plant communities. Environmental conditions associated with high flood frequency or long land use duration favoured species with contrasting SLAs (in standing vegetation occupancy and abundance), biogeographic origin (all components of vegetation), and capacity for hydrochory (in standing vegetation occupancy and abundance). We found evidence that flooding acts as both a dispersal filter and an abiotic filter (Fig. 1), consistent with the work of Leyer (2006) and Catford & Jansson (2014). Land use history acted as an abiotic filter in the studied wetland (Hobbs & Norton, 2004). Where species' trait-based responses differed among soil propagule banks, standing plant occupancy and abundance models (e.g. hydrochores and annual life spans), we identified that filtering was taking place at the abiotic rather than dispersal level (Fig. 1).

4.1 Species' trait-based responses to land use and flood frequency differ

Plant communities in fields with longer land use duration were characterised by species with high SLA, annual life histories, and herbaceous growth forms (i.e. non-woody). These characteristics are typical of colonizers, which dominate early succession (Kyle & Leishman 2009; Fournier et al. 2015). The interaction between hydrochory and land use duration was positive in the propagule bank but negative in the standing vegetation. These opposing relationships suggest that the relative scarcity of hydrochorous species in fields subjected to longer land use is not because of dispersal limitation, but due to abiotic (or biotic) conditions that inhibit colonisation. Abiotic filters may have been generated by fields with a long history of land use having higher elevations than fields with short land use duration (Appendix 3; Dawson et al. 2016), meaning that these fields would generally experience less frequent and shorter flood events. While we cannot discount the role of biotic filters, it is likely that biotic interactions (especially competition) are less influential in shaping the functional composition of the communities in fields that experienced long land use duration, i.e. these communities are characterised by high SLA and annual species, which tend to be poor competitors (Catford & Jansson 2014). The decline in native occupancy and abundance in the standing vegetation with increased land use durations, along with increases in exotics, suggest that a history of sustained land use imposes strong abiotic filters (such as soil factors), which are less suited to wetland native species and may favour exotic generalist species (Fig. 1; Hobbs & Norton 2004; Catford & Jansson 2014). Increases in exotics could also partly result from high propagule numbers of exotic species dispersing from the surrounding cultivated landscapes where they dominate. Given high correlations between land use duration and time since land use event, trait-based trends could also be driven by slow restoration rates in fields with long histories of land use (e.g. van der Valk et al. 1992; Stroh et al. 2012). Insufficient time for standing vegetation communities to progress beyond early succession (e.g. Aronson & Galatowitsch 2008) may affect observed patterns in the fields with longer land use duration, given surveys began three years after re-instatement of flood regimes. There may also have been insufficient time, or too few flooding events, for natives to accumulate in the propagule bank of these fields (van der Valk 1992; Middleton 2003, Dawson et al 2017b).

Natives increased with increasing flooding in the three models, whereas the abundance of exotics in the standing vegetation decreased with greater flooding. As both propagule bank and standing plant communities exhibited the same responses to flooding (in contrast to their responses to land use), dispersal, abiotic and biotic filters may have all promoted natives over exotics in frequently flooded areas (Fig. 1; Catford et al. 2011; Catford et al. 2014). For example, more native wetland species may be dispersed on floodwaters, may require flooding during some part of their lifecycle, and may be better competitors than exotics in more frequently flooded environments (Catford et al. 2011). However, we cannot identify to what extent each filter is acting in our study. Hydrochorous species responded positively to increasing flooding, possibly due to the increased frequency of dispersal events and greater environmental suitability (Nilsson et al. 2010). However, we recognize that we were only able to focus on primary dispersal methods of plants, with many species also using secondary dispersal traits (e.g., zoochorous seeds that can also be hydrochorous). This means that where our results suggest an environmental barrier with primary dispersal (e.g., zoochores decreasing with increasing flood frequency), a zoochorous species with a secondary dispersal method may overcome this.

4.2 Community Assembly

Many studies of wetland vegetation communities have combined surveys of standing vegetation and propagule banks (Grelsson & Nilsson 1991; van der Valk et al. 1992; Amiaud & Touzard 2004; Gurnell et al. 2006). To our knowledge, however, they have not previously been used to investigate trait filtering in plant community assembly. Functional trait approaches are generally underrepresented in restoration ecology literature (11% of studies examined community functional composition in Brudvig's 2011 restoration meta-analysis), despite their ability to inform on strength of filters, assembly rules and generalities across ecosystems (McGill et al. 2006; Brudvig & Damschen 2011; Laughlin 2014). By comparing trait differences in propagule banks, standing vegetation occupancy and abundance models, we found that flooding and land use may affect different community assembly filters and in contrasting ways.

Although our results showed strong trait-based trends, indicative of underlying assembly rules, there were some limitations with our study. We tested for trait convergence in our communities, but not for trait divergence (Belyea & Lancaster 1999; Weiher & Keddy 2011). Further, we may not have detected patterns produced when trait convergence and divergence act simultaneously in opposite directions, as these opposite trends would result in a neutral result overall (i.e., neither positive or negative interactions; Keddy 1992; Weiher & Keddy 2011; Götzenberger et al. 2012). While beyond the scope of this paper, tests for trait divergence could be conducted using different null models (Götzenberger et al. 2016), the results of which could be compared with our study to possibly disentangle abiotic and biotic filtering. Lastly, we only assessed the traits of seeds and adult plants and did not differentiate traits across the lifecycle or examine the importance of intraspecific trait variability. Although interspecific variation is likely more important for restoration (Andrade et al. 2014), incorporating intraspecific trait variation could potentially account for more total variation among sites, increasing the probability of detecting key community assembly filters (Bolnick et al. 2011; Andrade et al. 2014).

Notwithstanding these limitations, there are three generalities that can be drawn from this and other studies in relation to community assembly in modified wetlands:

1. increasing the duration and intensity of land use favours species with high SLA (a trait characteristic of early colonisers; Kyle & Leishman 2009; Fournier et al. 2015), presumably because either early colonising species with rapid growth rates typically perform well in disturbed areas or high SLA species are filtered out in less disturbed areas;
2. richness and abundance of native wetland species are positively related to flood frequency and negatively related to land use intensity (van der Valk et al. 1992; Galatowitsch & van der Valk 1996; Middleton 2003). This trend likely reflects adaptations of natives to flooding, but not to human land use, which favours exotic species better adapted to modified conditions;
3. trait-environment interactions are most strongly reflected in abundance of standing vegetation, given they have passed through all community assembly filters (Fig. 1; Götzenberger et al. 2012), as seen in our standing vegetation abundance models, which were the most significant, despite the lowest sampling effort.

4.3 Restoration management implications and trait-environment filtering

Understanding trait-environment interactions can identify mechanisms underpinning restoration, and can help to predict the relative success of interventions and to set realistic restoration goals (Keddy 1999; Laughlin 2014). We found support for the predictions of our conceptual model, with long land use duration associated with undesired species (i.e., exotics, fewer hydrochorous (wetland-specialist) species and high flood frequencies associated with desired species (i.e., natives and hydrochorous species). Manipulation of assembly filters may improve restoration of floodplain wetlands by biasing selection towards certain types of species (Catford & Jansson 2014; Laughlin 2014). Increasing flood frequency by using environmental flows to mimic natural regimes, may improve restoration outcomes by increasing native, hydrochorous and perennial species (Table 2; Catford et al. 2011; Catford et al. 2014). In often-cultivated fields, introduction of woody native species could also enhance restoration rates, as there were fewer woody species in the standing vegetation. Further, manipulation of abiotic gradients (e.g., flooding) may prevent dominance by generalists over specialists (e.g., species capable of tolerating many conditions as opposed to wetland species), especially in the early stages of restoration (Stroh et al. 2012; Fournier et al. 2015). In the Macquarie Marshes, restoring flood frequencies with environmental flows, similar to historic regimes, is likely to be most effective at restoring native wetland plant communities.

Authors' Contributions

Study design and development: SKD & JAC, Statistical design and application: DIW & SKD, Fieldwork and trait measurements: SKD, Manuscript design and writing: SKD, JAC, RTK, PB, DAK & DIW

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Data accessibility

All collected trait data are available in Appendix 5 and from the Dryad Digital Repository http://dx.doi.org/10.5061/dryad.bp79f (Dawson *et al.* 2017c). Any data resulting from field conducted for this paper will be submitted to the TRY database.

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Table 1: Descriptions of traits examined, their predicted interaction with human mediated gradients, supported by references (full references in Appendix 4).

Trait	Trait interpretation and reason chosen	Prediction with increasing land use/*flood*	References
Specific Leaf Area (SLA; mm^2 mg^{-1})	Common core trait, often used in wetlands, related to plant growth rate and competitive ability	Increase / *Increase*	Weiher et al. 1999, Pierce et al. 2012, Pérez-Harguindeguy et al. 2013
Seed mass (gm)	Common core trait, larger seeds can confer higher competitive ability, survival rate, resilience, decreased propagule bank persistence; more likely to be hydrochorus or zoochorus and less likely to be found at higher water depths	Increase / *Increase*	Weiher et al. 1999, Pywell et al. 2003, Moles & Westoby, 2004, Moles et al. 2005, Pérez-Harguindeguy et al. 2013, Catford & Jansson, 2014
Native provenance	Important indicator of restoration (target species); riparian/ floodplain areas are vulnerable to exotic invasion, particularly after alteration to natural flood regimes	Decrease / *Increase*	Catford et al., 2011, Catford & Jansson, 2014
Primary dispersal mode	Common core trait, can inform on how plants disperse to sites, how far they can travel and likely final destinations;	Hydrochores: Decrease / *Increase* Zoochores: Increase / *Decrease*	Weiher et al. 1999, Belyea & Lancaster, 1999, Gurnell et al., 2006, Leyer, 2006, Nilsson et al., 2010,

	relatively understudied; hydrochory especially important in wetland vegetation structure; note: wind not used due to correlations with hydrochory		Götzenberger et al., 2012, Pérez-Harguindeguy et al. 2013, Catford & Jansson, 2014
Longevity (annual/perennial)	Common core trait, important characterisation in wetlands; associated with recolonisation after flood; especially exotics and may be found in early succession after disturbance; longer life spans (perennials) associated with persistence in the community	Decrease/ *Increase*	van der Valk, 1981, Keddy & Boutin, 1993, Weiher et al. 1999, Amiaud & Touzard 2004, Kyle & Leishman 2009, Merritt et al., 2010, Lunt et al., 2012, Pérez-Harguindeguy et al. 2013, Catford et al., 2014
Woody (life form = tree or shrub)	Indicates secondary succession and target restoration species (*Eucalyptus camaldulensis* and *Duma florulenta*); reduced/missing tree and shrub species associated with degraded riparian areas; also associated with ecophysicological adaptation including maximising photosynthetic production	Decrease / *Increase*	Kyle & Leishman 2009, Merritt et al., 2010, Pérez-Harguindeguy et al. 2013

Table 2: Supported (bold), unsupported (italicized) and unresolved (plain) predictions of trait-environment interactions for the seven traits (Table 1), separately for land use duration and flood frequency drivers.

Trait	**Response to increasing land use duration**	**Response to increasing flood frequency**	**Implications for community assembly**	**Implications for restoration**
SLA	**Increase**	Increase	Indicates primary succession/ competitive exclusion, potential biotic filtering	Decreasing restoration rates with higher land use
Seed weight	**Increase**	Increase	Indicates heavier seeds have advantage in propagule banks of higher land use duration	
Native	**Decrease**	**Increase**	Indicates higher land use duration alters filters to detriment of natives. Indicates natives possess traits enabling survival at higher flood frequency	Increasing flood in higher land use fields may increase natives
Hydro-chore	***Decrease***	**Increase**	Conflicting results between standing vegetation and propagule bank with land use indicate abiotic/biotic filtering. Flood acting as dispersal/ abiotic filter for hydrochores	Increasing flood in higher land use duration fields may increase hydrochores (desired plant group)
Zoo-chore	*Increase*	**Decrease**	Less animal dispersal than expected in higher land use	Flood demonstrates opposite dispersal filter to hydrochores

Annual	**Increase**	***Decrease***	Indicates primary succession in higher land use. Conflicting interaction with flood indicates more species with lower abundances	Decreasing restoration rates with higher land use. Increasing flood may increase abundances of perennials
Woody	**Decrease**	Increase	Indicates early succession with higher land use; woody species have not recolonised yet	Woody species take a longer time to recolonise; may need to be planted

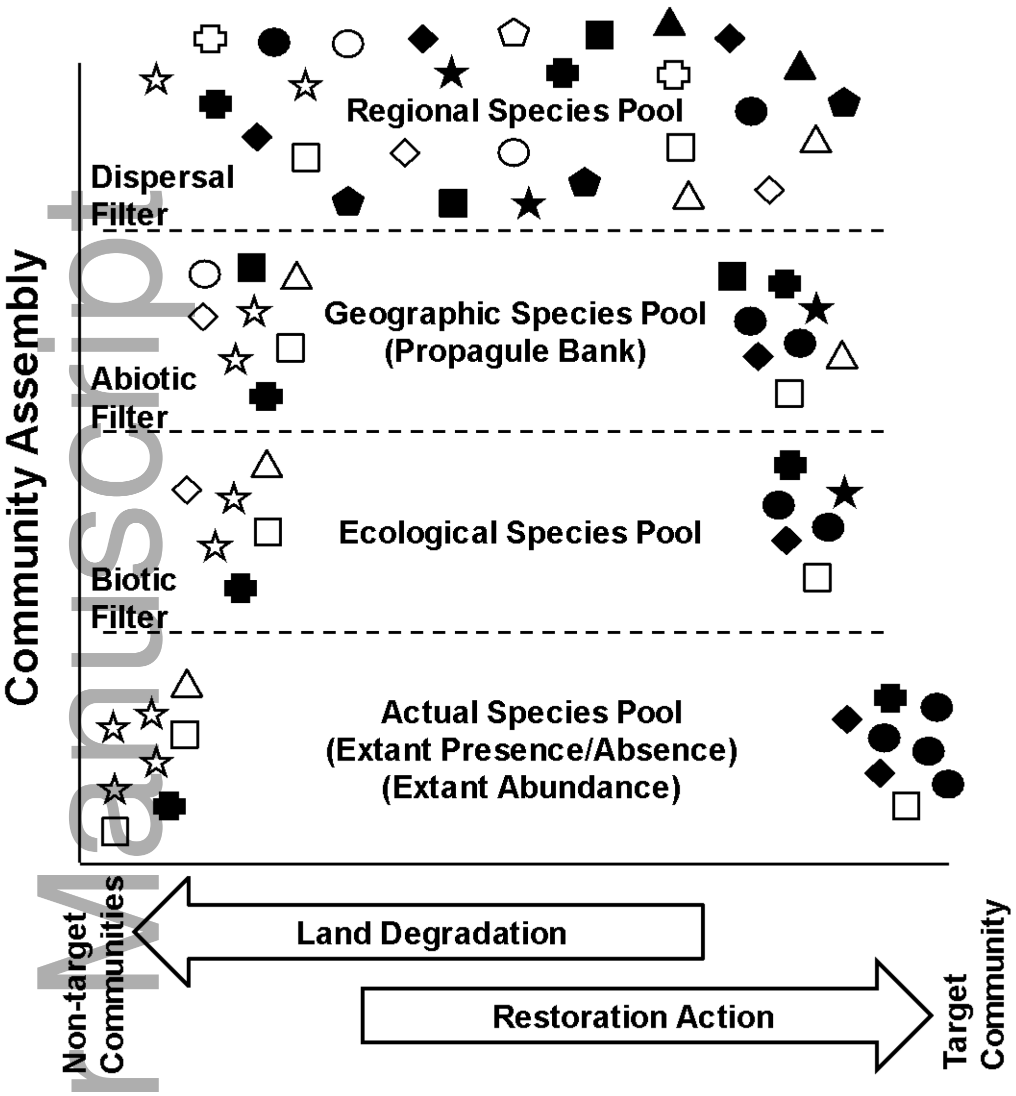


Figure 1: Conceptual diagram indicating how vegetation assembly varies with opposing influences of land degradation (land use duration) and restoration action (flooding), in relation to the three filters (dispersal, abiotic and biotic). We assumed that with more flooding there would be an increased likelihood of achieving target communities (i.e. mainly comprised of target species; filled symbols), however with increasing land degradation there would be a higher chance of outcomes with non-target or undesired species (unfilled symbols) dominating communities. In the example depicted here, dispersal has the major influence on restoration outcomes, which will change depending on the community (modified from Belyea & Lancaster 1999; Götzenberger et al. 2012; Catford & Jansson 2014).

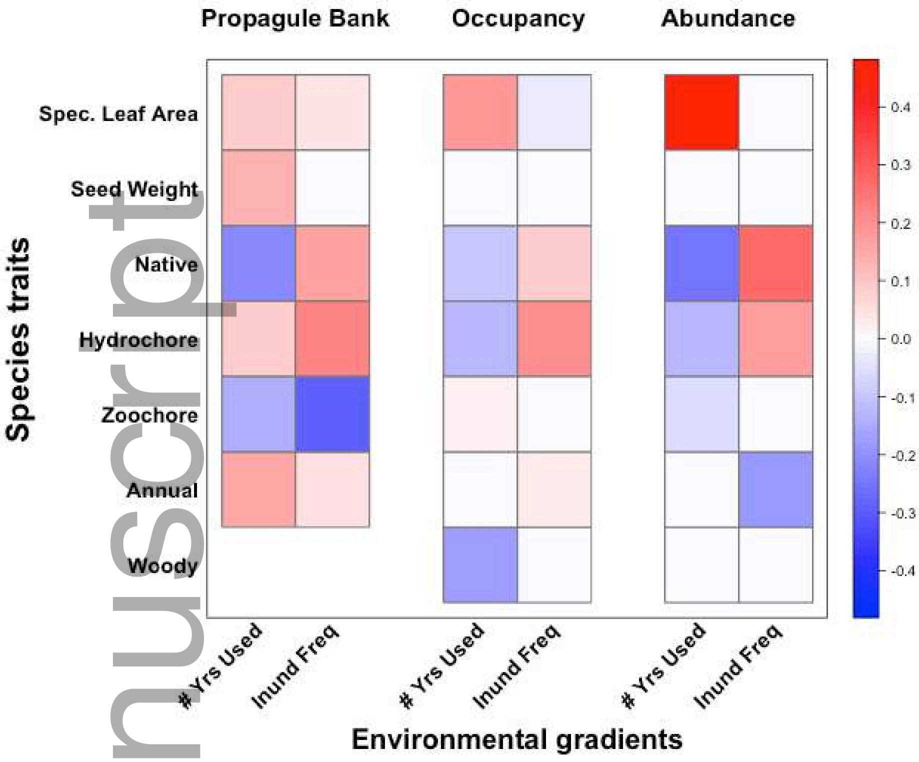


Figure 2: Fourth-corner modelling results for plant trait interactions with human mediated gradients of land use duration and flood frequency. Each pair of columns from the three model (soil propagule bank, standing vegetation occupancy and abundance) represents interactions between traits and the human mediated gradients of land use duration and flood frequency. Colour grading show the direction and strengths of standardized coefficients of fourth-corner models for all environment/trait interaction terms from GLM-LASSO modeling. Red and blue indicates positive and negative associations respectively, colour intensity reflects relationship strength. For example, a value of 0.4 in the standing vegetation abundance model between SLA and flood frequency indicates the abundance vs. SLA slope increases by 0.4 for every unit (standardised) increase of flood frequency. As data going into models differs we cannot compare interaction strength between models.

Figure 3: Traits with >|0.2| interaction strength in Fig. 2 (after LASSO selection), for models fitted to the propagule bank model (a-c) or the standing vegetation abundance model (d-e) with 95% confidence interval showing predicted counts of binary traits (logged), along the human mediated environmental gradients from models fitted with the other environmental gradient held at mean value and no other trait interactions; where # of Years Used was the number of years a field was either cleared or cultivated and; # Flood Frequency was the

number of floods that reached that site from 32 flooding events over 25 years.

Supporting Information

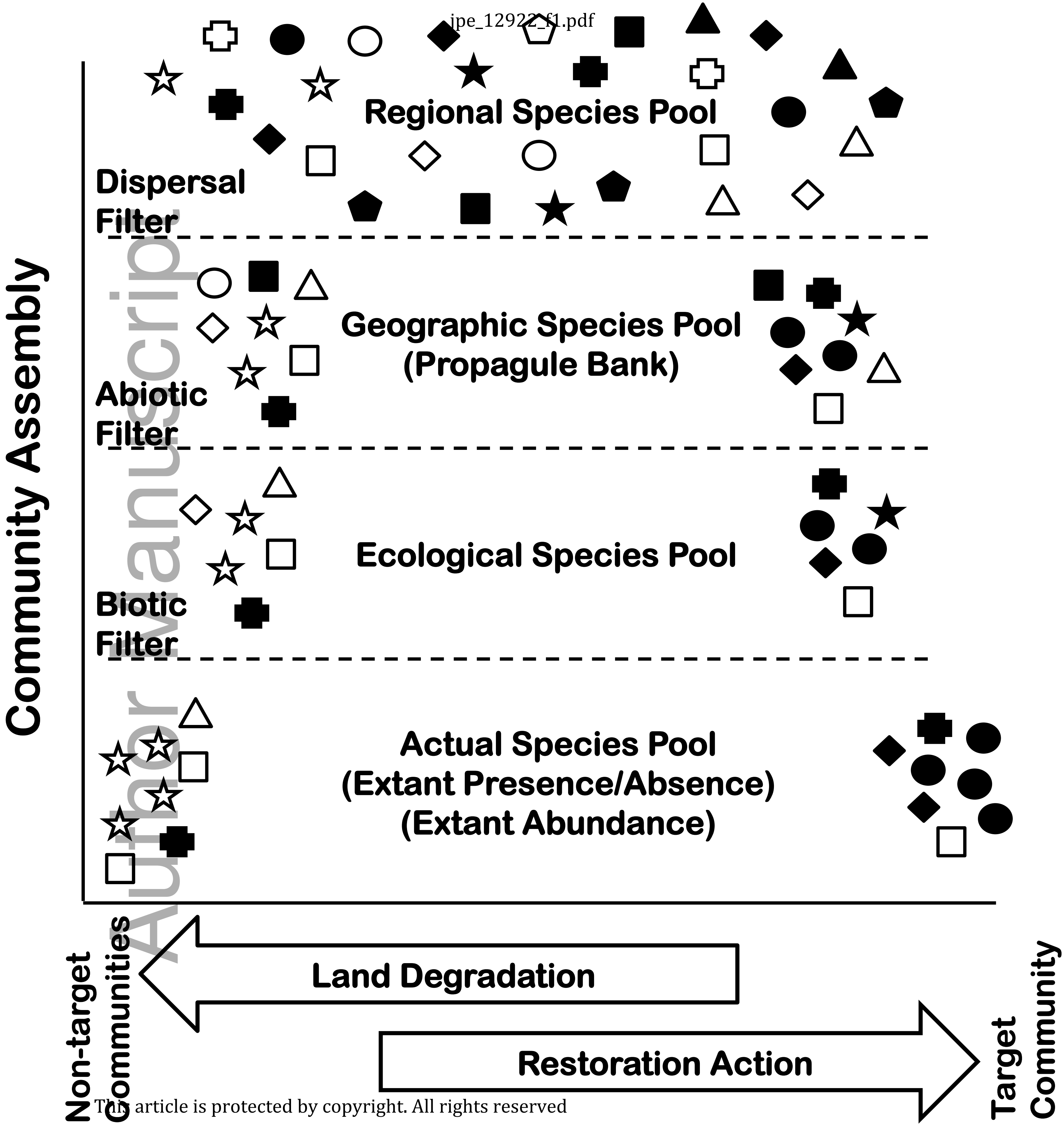
Appendix 1: Details on field history and flooding frequency at each site

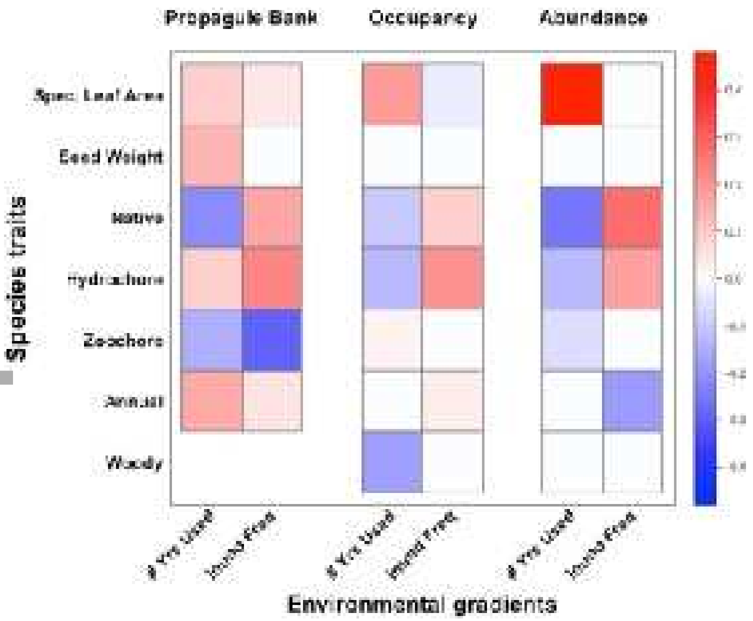
Appendix 2: Pictures from each of the 12 fields of Pillicawarrina

Appednix 3: Correlation plots between traits and between environmental variables for each of the three datasets

Appendix 4: Reference list for Table 1 and sources of information for Appendix 5

Appendix 5: Species traits and data source used in the analysis


Regional Species Pool
Dispersal Filter
Geographic Species Pool (Propagule Bank)
Abiotic Filter
Ecological Species Pool
Biotic Filter
Actual Species Pool (Extant Presence/Absence) (Extant Abundance)
Community Assembly
Land Degradation
Restoration Action
Non-target Communities
Target Community



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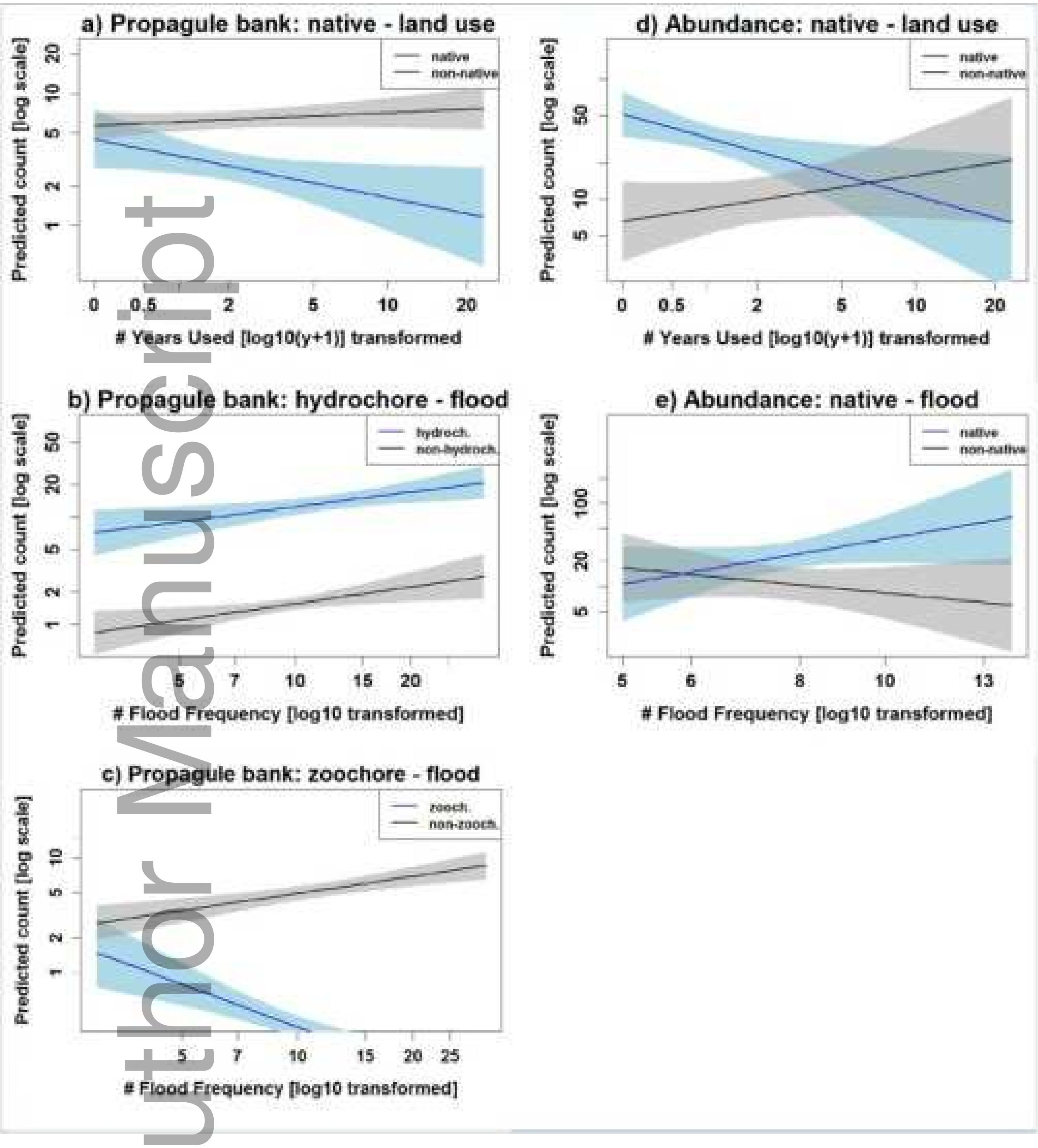

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