



## Predicting dispersal-limitation in plants: Optimizing planting decisions for isolated wetland restoration in agricultural landscapes



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### ABSTRACT

Isolated wetlands are often degraded by agriculture, increasing sediment accretion and altering plant composition. Two common opposing wetland restoration practices are self-design vs. intensive revegetation. Self-design restores hydrogeomorphology without inoculating wetland taxa into restoration sites. Self-design may not meet restoration targets if dispersal-limited plants do not colonize restoration sites. Alternatively, intensive revegetation (hydrogeomorphic restoration combined with revegetation) is costly and time consuming. We investigated plant dispersal-limitation in 309 isolated wetlands among two agricultural landscapes in the U.S. Great Plains (the western High Plains (WHP) and the Rainwater Basin (RWB)) and three land-uses (reference, croplands, and previous croplands) to predict optimal restoration practices. We present analytical tools predicting whether self-design or intensive revegetation will be more successful elsewhere. In the WHP and RWB, perennial wetland cover was 61% and 31% greater in reference than in other land-uses. Distance to the nearest reference wetland explained perennial wetland richness in both regions, and area of reference wetlands within 15 km also was important in the WHP. Annual wetland species were over-represented in previous cropland wetlands and were less influenced by landscape isolation. We analytically identified dispersal-limited and cosmopolitan species in reference wetlands, with distance to reference wetlands and area of surrounding reference wetlands important in determining composition. Further, dispersal-limited plants in reference wetlands had greater cover in clustered than isolated wetlands in previous croplands. Plant community patterns in reference conditions may predict composition in restored wetlands. This aids selection of self-design or revegetation restoration approaches for individual plant species in isolated wetlands.

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### 1. Introduction

Loss of wetlands is pervasive in the United States (Dahl, 2000) and worldwide (Finlayson et al., 1999). Many remaining wetlands have been impacted by conversion of watersheds from native to agricultural conditions (Brinson and Malvárez, 2002). This is particularly true of isolated depressional wetlands globally (Brinson and Malvárez, 2002). We define isolated wetlands as those in indi-

vidualized catchments, often containing groundwater connections, but lacking surface water connections to other aquatic areas under normal conditions. Isolated wetlands are estimated to account for 20% of the numerical total of wetlands in the United States (Tiner et al., 2002), though comparable estimates elsewhere are lacking. Isolated wetlands are especially vulnerable to agricultural conversion because they occur in flat, fertile landscapes, encouraging wetland drainage and infilling (Smith et al., 2008). Further, isolated wetlands frequently dry seasonally and are readily cultivated when dry. In this paper, we describe common opposing practices to restore vegetation communities in isolated wetlands and generate analytical models for predicting optimum restoration methods.

Isolated wetlands are important because of services they provide generally common to wetlands, including carbon storage capacity, flood water mitigation, habitat for wetland biota, and water purification (Tiner, 2003; Smith et al., 2008). Further, isolated wetlands maintain stable meta-populations among nearby wetland patches (Hanski, 1998; Tiner, 2003). Isolated wetlands also provide important stopover sites for migrating wildlife.

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Two philosophies for wetland restoration currently are practiced. The first is based on self-design (Mitsch et al., 1998). This restoration technique relies on unaugmented colonization by organisms to sites following hydrology and geomorphology restoration. Self-design has also been called the “Field of Dreams” hypothesis: “If you build it, they will come” (Hilderbrand et al., 2005). This hypothesis suggests that after restoring abiotic processes, organisms self-assemble. For example, in agricultural isolated wetlands, restoration by self-design involves plugging ditches or drainage tiles that de-watered wetlands for cultivation. Removal of upland sediments from wetlands and grading to restore microtopography also are common (Galatowitsch and Van der Valk, 1998). Wetland plant communities then are expected to develop from seed banks and dispersal.

However, self-design approaches have been criticized (Streever et al., 2000; Galatowitsch, 2006) because dispersal of some plants may be limited (van Dorp et al., 1996; Galatowitsch, 2006). For example, wetland plants requiring moist habitats may be dispersal-limited because of lower establishment in intervening non-wetland habitat (Tiner, 1991). Further, perennial plants should be more susceptible to landscape isolation than annuals because perennials generally are *k*-selected whereas annuals are *r*-selected (Pianka, 1970). This previous statement theorizes concerning average plant traits, but we present analytical tools for determining traits of individual species. Perennials were called *k*-selected because they are long-lived, slow-growing and competitive in stable environments. Perennials also produce fewer offspring annually (Pianka, 1970; Hautekèete et al., 2001; Bonser and Aarssen, 2006). Annuals conversely, are short-lived, competitive in fluctuating or disturbed conditions, and produce many offspring in one breeding episode. Species rarely are strictly *r*- or *k*-selected, but fall somewhere on the continuum between extremes (Pianka, 1970).

Thus, we expect reduced wetland perennial colonization in disturbed environments such as croplands. Further, perennial seed sources should also be reduced in cropland seed banks because plowing annually removes adults before seed production. We term this model the dispersal-life history wetland plant model. By life history, we mean annual vs. perennial life history strategies. Foundations of this model have been described by others (Godwin, 1923; Zedler, 2000; Ozinga et al., 2005; Galatowitsch, 2006; Poschlod et al., 2007). Our model assumes that the probability of a propagule reaching a given location increases with the number of propagules produced. As a result, lower yearly rates of perennial seed production reduce the probability of perennial dispersal to distant locations, assuming other confounding factors such as seed size, growth form and dispersal mode are equivalent. Thus, the model predicts, that relative to reference wetlands, perennial wetland plants will be underrepresented and wetland annuals over-represented in agricultural wetlands, or wetlands with a past history of disturbance, such as new restoration sites where agriculture previously occurred. Dispersal capabilities of individual species of course may vary. Therefore, in this paper we quantify both general traits and individual species responses.

A wetland restoration approach addressing dispersal-limitation is more time and materials intensive than self-design. The intensive approach involves introducing organisms into restoration sites following restoration of hydrology, usually by seeding or transplanting from nearby reference sites (Streever et al., 2000). Seeding or planting has the advantage of jump-starting plant assembly, potentially reducing establishment of introduced species (Zedler and Kercher, 2005). Further, high initial restoration investments sometimes increased restoration success (Klimkowska et al., 2007). We use “introduced” as defined by the USDA PLANTS database (e.g. plants occurring outside their native range) (USDA and NRCS, 2010). Disadvantages of the intensive approach include ex-

pense, failure of some transplants to establish, and potential failure of restored sites to resemble natural communities (Zedler and Kercher, 2005; Noël et al., 2011). The latter is particularly true if plants are not local genetic varieties or establish disproportionately to native abundance (Zedler and Kercher, 2005).

Intensive revegetation and self-design restoration approaches are currently practiced globally (e.g., Klimkowska et al., 2007; Poschlod et al., 2007; NRCS, 2008). Ideally, we would like to predict effective restoration methods to increase efficiency and the probability of reaching restoration goals. We will explore the applicability of the dispersal-life history wetland plant model to aid restoration of isolated wetlands. We investigated this model in two landscapes where isolated wetlands and agriculture occur in high density. We compare effects of landscape isolation on wetland plant communities within major land-use categories to elucidate general principles. These land-use categories are reference land-use (i.e., that with the least history of anthropogenic disturbance), wetlands within row-crop agricultural lands, and wetlands within croplands that have been taken out of production. This latter land-use lends insight into community assembly after agricultural disturbance has ceased, similar to what might occur in self-design restoration.

We develop analytical approaches that use extant plant communities in reference wetlands to predict the best restoration practice in regions of interest. We test these predictions using plant communities in wetlands in previous croplands. Our approach analyzes the degree to which landscape isolation may limit plant dispersal for individual plant species. Should isolation be strongly influential, we suggest revegetation is more likely to establish that species in restoration communities than self-design. Our approach is useful because it may identify the best restoration strategy for individual species of concern before restoration is initiated.

## 2. Materials and methods

### 2.1. Study area

We surveyed plants in isolated wetlands, called playas, within two regions of the U.S. Great Plains: the western High Plains (WHP) and the Rainwater Basin (RWB) (Fig. 1). These regions differ in dominant vegetation, land-use history and climate (Smith, 2003). Playas in both regions have hydric clay Vertisol soils and are freshwater, recharge wetlands. As such, hydrologic inputs to playas are precipitation and overland sheet flow, while outputs are limited to evapotranspiration and groundwater recharge (Smith, 2003). Playas are temporary to seasonal wetlands, remaining wet for weeks to months (Smith, 2003). RWB playas are wetter than WHP playas and typically inundate from 1 to several months (Wilson, 2010). Individual playas inundate unpredictably and remain dry for indeterminate periods (Smith, 2003; Wilson, 2010). When dry, playas contain upland prairie vegetation, but seed banks and immigrating propagules rapidly transform playas into wetland plant communities following inundation. Playas in both regions are dominant surface freshwater features because rivers and lakes are rare (Smith, 2003; Wilson, 2010).

The WHP, a 30 million ha sparsely settled landscape, is a short-grass prairie eco-region encompassing six states. Climate in the WHP is semiarid with precipitation varying from 38 cm to 63 cm along a west–east gradient (Smith, 2003). Playas average 7 ha (S. McMurry, unpublished data) and are generally round in shape. Up to 60,000 playas occur in the WHP (Playa Lakes Joint Venture, <http://pljv.org/>). We investigated three land-uses in the WHP, native short-grass prairie (covering ~12 million ha of the region), row-crop agriculture (~15 million ha) and croplands taken out of production (~3 million ha) (O'Connell et al., 2012). This latter

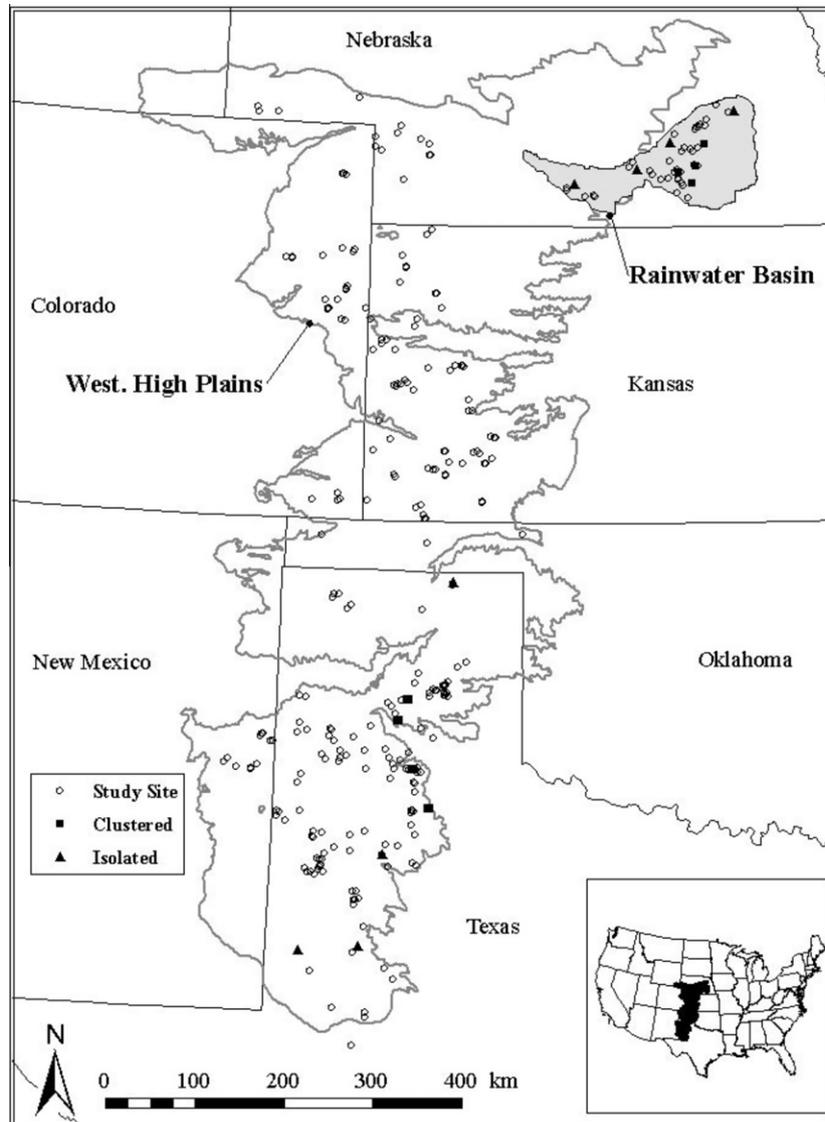


Fig. 1. Locations of study wetlands in the WHP and RWB, USA.

land-use is governed under the United States Department of Agriculture (USDA) Conservation Reserve Program (CRP). The CRP began in 1985 and removes highly erodible agricultural lands from production by establishing perennial grass cover. This land-use shares features with restoration in that crop production was ceased and the catchment replanted to upland grasses. However, CRP lands rarely resemble short-grass prairie because CRP mostly planted monocultures of introduced tall-grasses in the WHP (O'Connell et al., 2012). Wetland plant species were not planted in CRP playas and geomorphology was not restored (e.g., agricultural sediments were not removed). CRP playas catchments were established from 1 to 20 years prior to surveys. Species richness in CRP playas is greater than in cropland playas and equivalent to grassland playas, but plant composition does not resemble grassland playas (O'Connell et al., 2012). True restoration of playas in the WHP is limited to date. However, community composition in CRP playas lends insight into plant assembly after cultivation ceases.

Other land-uses surveyed were cropland catchments, containing row-crop agriculture. Cropland playas frequently were cultivated when dry. We used native, never plowed short-grass playa catchments as our reference condition in the WHP.

The RWB is located in south-central Nebraska (Fig. 1). Climate is more temperate than in the WHP, with greater precipitation, averaging 130 cm yearly (Wilson, 2010). Playas remaining in the RWB are larger than those in the WHP, averaging 15.6 ha (S. McMurry, unpublished data), and irregularly shaped. The RWB, part of the central plains eco-region, occupies roughly 1.5 million ha, 1.2 million of which are row-crop agriculture. Approximately 1800 playas, fewer than 10% of historic playas, remain (Rainwater Basin Joint Venture, [www.rwbjv.org](http://www.rwbjv.org)). The RWB was originally mixed- to tall-grass prairie, but unlike the WHP, little native prairie is left. Therefore, our reference condition in the RWB is the best available: unplowed playas with some grass buffer (>200 m) between surrounding croplands. Grass buffers did not cover the catchment majority as in the WHP. In addition to reference and cropland playas, >2000 ha of RWB wetlands are in the USDA's Wetland Reserve Program (WRP). The WRP program was initiated by USDA under the Farm Bill in 1990. For WRP restoration in the RWB, cultivation was ceased and eroded agricultural topsoil was removed to restore hydrology. Plants passively recolonized. Sediment removal occurred between 1 and 12 years before surveys. This represents self-design restoration.

## 2.2. Plant composition surveys

We used GIS databases of probable playa locations to randomly select survey playas (A. Bishop, USFWS, Rainwater Basin Joint Venture, and Playa Lakes Joint Venture). In the WHP, 261 playas were surveyed (86 each in cropland, CRP and grassland). In the RWB, 48 playas were surveyed (16 each in cropland, grassland and WRP; Fig. 1).

We estimated plant composition and cover using step-point surveys (Evans and Love, 1957). Step-point surveys spanned playa diameter along two transects. Surveys involved identification of plants encountered at each step, generating point-cover estimates approximately every 1 m. We surveyed playas twice to identify cool (surveyed 10 May–30 June) and warm-season species (surveyed 10 July–31 August) (Smith and Haukos, 2002). We collected voucher specimens to verify unknown plants. We recorded whether playas were wet (inundated or surface moist from past inundation) or dry during surveys.

We list species names as defined in the USDA PLANTS database (USDA and NRCS, 2010), which largely uses taxonomy from the Biota of North America (Kartesz, 2011). We used USDA PLANTS to classify plants according to life history (annual or perennial) and according to water tolerance (e.g., wetland indicator status: wetland obligates, facultative wetland species, through upland species). See O'Connell et al. (2012) for a detailed description of categorizing plants by wetland indicator status. Biennials were classified as perennials to simplify analyses. We calculated proportion of wetland cover of all objects encountered (plants, crops, bare ground and water) by adding encounters for each object over both transects and dividing by the total number of steps in both transects.

We refined species categorizations using guilds incorporating life history, water tolerance and zone of occurrence within wetlands, following Galatowitsch (2006). See Appendix 1 for species categorizations and methods. To test our hypothesis that wetland perennial species were dispersal-limited and require planting in restoration sites, we used an analytical approach. We first compared perennial guild cover among land-use types. We further identified relationships among species richness and wetland isolation. We next identified patterns of occurrence for individual plant species in reference conditions as explained by wetland isolation. We then used patterns identified in reference conditions to predict cover of individual species in previous croplands. If we can predict species cover, then we have pre-knowledge of which species may require planting in restoration sites.

## 2.3. Differences in composition, proportion of cover and species richness of perennial guilds among land-use

To determine if perennial guild composition differed between reference, croplands, and past croplands, we compared plant composition (proportion of total wetland cover for each species) with partial canonical correspondence analysis (pCCA) (CANOCO 4.5, Biometris, Wageningen, The Netherlands). Canonical correspondence analysis (CCA) is a special case of multivariate regression (Palmer, 1993), and uses multiple linear least-squares regression to assess relationships of weighted species averages among samples sites along environmental gradients. pCCA is a type of CCA, where variation resulting from covariables is factored out, leaving behind variation from variables of interest (ter Braak, 1988). We used survey time (early or late growing season), playa wetness (wet or dry) and latitude and longitude as covariables. This allowed us to determine differences in plant composition among land-use above and beyond that caused by these covariables. We used CANOCO to down-weight rare species. This is good general practice because we have incomplete information concerning rarely ob-

served species and must be cautious interpreting relationships for them (ter Braak and Šmilauer, 2002). We square-root transformed species cover to reduce influence of outliers. We used CANOCO software to graph species comprising at least 3% of total samples and only interpreted graphed species (ter Braak and Šmilauer, 2002). We thus limited conclusions to common species observed throughout our study areas. For common species, favorable germination conditions were prevalent and environmental relationships can be modeled more reliably. We used CANOCO to test significance of canonical axes, using Monte Carlo simulation with 999 permutations under the reduced model (Verdonchot and ter Braak, 1994). Monte Carlo permutation tests are useful because their only assumption is that data are independent. We plotted species by guild and visually compared number of species in each guild among land-uses. Species names are shown as the first four letters of the genus and species; see Appendix 1 in Supporting Information for full species names.

We formalized this analysis by comparing cover of perennial guilds (wet prairie perennials, sedge meadow perennials, and shallow and deep emergent perennials) among land-uses. We used generalized linear models (GLMs) with binomial response and logit-link between model and response variable (glm procedure in R, version 2.12.1, the R Foundation for Statistical Computing). A detailed description of GLMs is provided by Zuur et al. (2009). For all GLMs, results were graphed and discussed on the scale of the data for ease of interpretation.

To determine if landscape isolation had significant relationships with richness of wetland perennial guilds in playas (i.e. wet prairie, sedge meadow, shallow and deep emergents) and wetland annual guilds (mudflat and shallow annuals), we used ArcGIS to extract distance to nearest reference playa (distance was from the surveyed playa boundary to the nearest reference playa boundary). We used only reference wetlands rather than all wetlands because preliminary analyses (not presented) suggested propagule source quality was important. Further, we buffered surveyed playas using fine (1 km), medium (5 km), or broad-scale (15 km) radii and extracted area of surrounding reference playas (excluding the surveyed playa) within the buffered region. Dispersal and distance from propagule sources are related (Okubo and Simon, 1989; Leng et al., 2009). We selected these radii because few playas are nearer than 1 km to each other and dispersal-distance relationships have been observed for distances ranging from 3 km (Galatowitsch, 2006) up to 14 km (Leng et al., 2010). We assumed greater areas of nearby wetlands increased dispersal events. Our assumption was based on metapopulation theory, which hypothesizes that populations in small discrete habitat patches, such as isolated wetlands, have higher probability of undergoing local extinction without immigration from nearby habitats (Hanski, 1998). A justification and a supporting analysis for our assumption can be found in Appendix 2. Further, similarity among vegetation communities and distance between communities has been used as a proxy for dispersal-limitation by others (Leng et al., 2009).

Thus, we used regression of species richness on landscape isolation variables to infer dispersal-limitation. We used GLMs (Poisson error and log-link between model and response variable, see Zuur et al. (2009)) to compare species richness of wetland plants (facultative wetland through wetland obligates) among land-uses and landscape isolation for both annual and wetland species. The explanatory variables for this analysis were distance to the nearest reference playa, area surveyed within the playa, area surveyed \* land-use interaction, playa inundation, area of surrounding playas (within 1, 5, or 15 km) and surrounding playas area \* land-use. Over dispersion was investigated and was not evident (Zuur et al., 2009). We used AIC model selection to rank models (R package MuMIn). We present the highest-ranked model in our results using coefficients averaged among models with  $\Delta AIC < 4$

(Anderson, 2008). We gave equal weight to all models with  $\Delta$  AIC < 4. We also present the proportion of explained variation in perennial and annual wetland plant richness by all candidate predictors. We use all candidate predictors (rather than just those in the best model) to remove bias from comparing models with different numbers of predictors. In GLMs, variation explained is determined by deviance (Zuur et al., 2009), where explained data variability is percent explained deviance, e.g.,  $[(\text{null deviance} - \text{residual deviance})/\text{null deviance}] * 100$ .

#### 2.4. Using reference wetlands to predict underrepresented plants in previous cropland wetlands because of dispersal-limitation

We wanted to determine whether plants identified as dispersal-limited in reference had predictably reduced cover in playas where agricultural disturbance had ceased. We compared plants categorized as dispersal-limited or cosmopolitan (e.g., not dispersal-limited and able to establish in isolated areas) in a pCCA of landscape metrics within reference conditions only. We assumed greater abundance in isolated wetlands implied species were good dispersers, whereas species maximally abundant in clustered playas were poor dispersers.

We used the same covariates, transformations, and inclusion rules as in the pCCA previously described. However, for this model we used manual selection in CANOCO to explore the best landscape metrics to incorporate. If area of surrounding playas was important, we included only the buffered zone explaining the greatest variation in plant communities in our final model.

This analysis designated environmental vectors representing degree of landscape isolation: (1) increasing distance from the surveyed playa to the nearest reference playa and (2) increasing area of surrounding playas. Environmental vectors in pCCA point in the direction of strongest correlation between species composition and the depicted variable. The length of the vector increases for stronger correlations. Plant species were plotted as species scores at their centroid of inertia (i.e., where they were maximally abundant with respect to environmental vectors). To identify where species load on vectors, one may draw a perpendicular line from species scores to the vector. Species not loading on a vector (on the opposite side of origin) occurred at the lowest values of that predictor.

We used the resulting reference playa graph to identify plants common in clustered playas (near to a reference playa and high area of surrounding reference playas). Plants common in clustered playas should load heavily onto the “surrounding playa area” vector and should be on the opposite side of the origin from increasing “distance to reference playa” vector. We categorized these plants as dispersal-limited, regardless of guild. We also identified plants common in isolated playas (far from reference playas and with little area of surrounding reference playas) and categorized these plants as cosmopolitan.

Next, we identified clustered and isolated playas in CRP (WHP) or WRP (RWB). To do this, we standardized distance to reference playas and surrounding playa area by converting them to z-scores:  $z = ((\text{observation} - \text{mean})/\text{standard deviation})$ . We multiplied z-scores for distance to reference playa by  $-1$  so that increasing (larger) values reflected clustered playas in both metrics. We added the standardized z-scores from both metrics together to generate an overall isolation metric. We then chose the four most isolated and clustered playas by identifying the four lowest and highest scores. We avoided including multiple playas within 20 km of each other in favor of the next most clustered playa, to ensure clustered study playas were in separate clusters. In the WHP, all of the clustered playas were in Texas. To minimize potentially confounding regional differences for this comparison, we also limited isolated playas to those in Texas. We used binomial GLMs (logit-link) with cover of either dispersal-limited or cosmopolitan plants as the re-

sponse variable and clustered vs. isolated playa as the predictor. As above, we present variation explained by the model as percent deviance.

### 3. Results

#### 3.1. Differences in composition, proportion of cover and species richness of perennial guilds among land-use

Plant composition differed along all canonical correspondence axes in the WHP ( $F = 25.58$ ,  $P = 0.0001$ ) and the RWB ( $F = 3.32$ ,  $P = 0.001$ ), suggesting composition differed among land-uses after survey time, location, and playa inundation were taken into account (Fig. 2a and b). Fewer species were common in croplands than in reference, WRP, or CRP playas. Plant guild composition also differed by land-use, with wetland perennial guilds under-represented in CRP, WRP, and cropland playas (Fig. 2a and b). Slightly more mudflat species were maximally abundant in croplands, CRP and WRP than in reference playas (Fig. 2a and b).

Cover of wetland perennial guilds was greater in reference than in in cropland and previously cropped playas in the WHP ( $P < 0.001$  for all model effects, Fig. 3a). In the RWB, generally, perennial guilds with greater water tolerance (least tolerance to intervening upland habitat) were most under-represented in agriculturally influenced watersheds ( $P < 0.0001$  for all model effects, Fig. 3b).

Wetland perennial richness differed by land-use and area surveyed \* land-use in both regions, such that area surveyed was important in croplands but not in other land-uses (Table 1). Further, landscape isolation influenced richness of wetland perennials, with wetland perennials richness negatively correlated with distance to reference wetlands in both regions (Fig. 4a and b). Surrounding playa area within a 15 km radius and playa inundation corresponded with species richness only in the WHP (Fig. 4a). Other candidate predictors did not explain variation in the data.

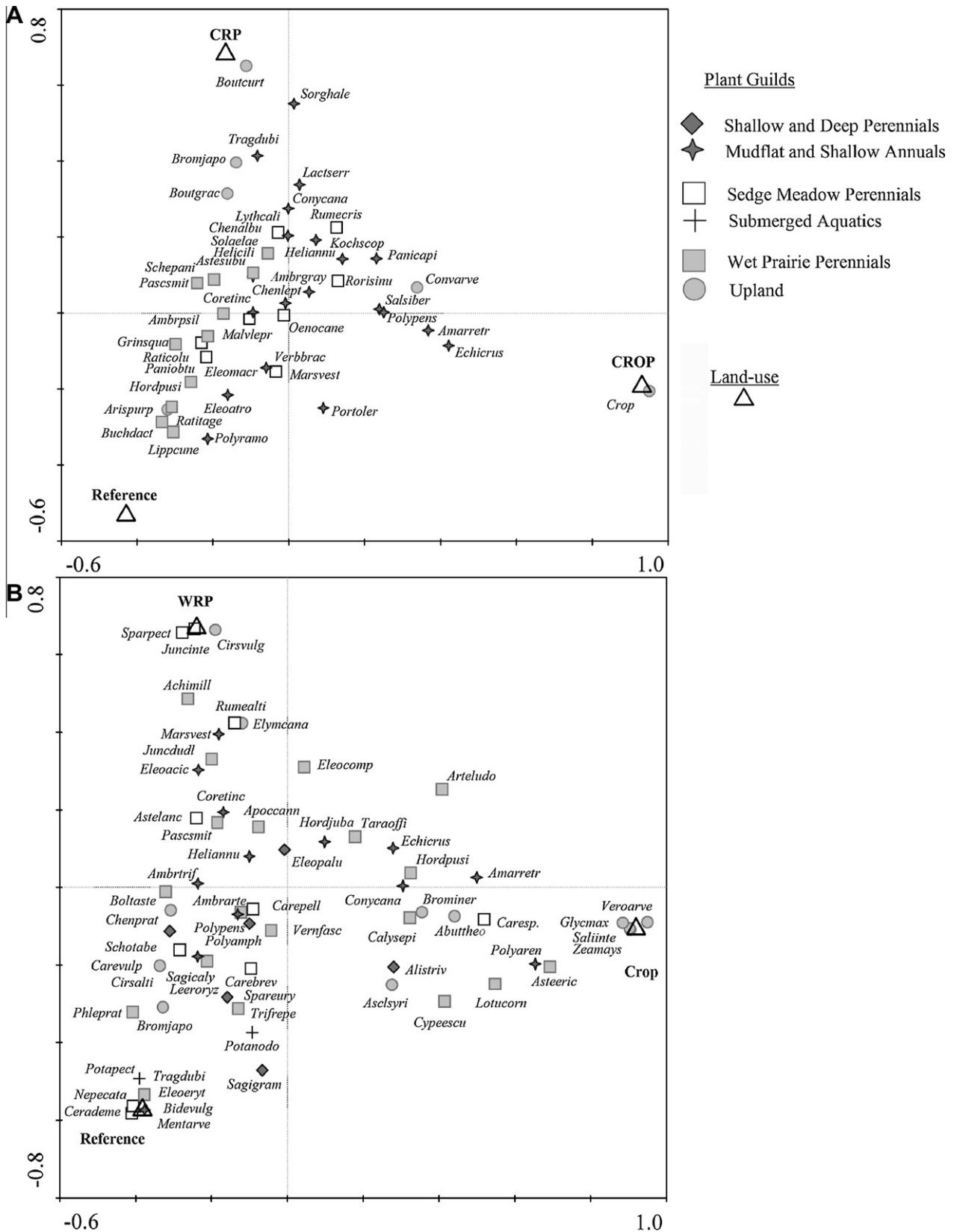
#### 3.2. Comparing annual and perennial richness to test the dispersal-life history wetland plant model

Annual wetland plant richness differed by land-use and area surveyed \* land-use in both regions (Table 2). Area of surrounding playas within 5 km and playa inundation increased annual wetland richness in the WHP, but landscape isolation variables and wetland inundation were not related to richness in the RWB.

Perennial wetland plants had reduced richness in previous croplands than in reference, while annual richness was similar between reference and previous croplands (Table 3). The ratio of annuals to perennials increased from reference to previous cropland wetlands, as predicted by the dispersal-life history wetland plant model. Further, geographic isolation (distance to reference, surrounding playa area) explained greater data variability for perennials than annuals (Table 3), supporting our hypothesis that perennial wetland plants may experience greater dispersal barriers.

#### 3.3. Using reference wetlands to predict underrepresented plants in previous cropland wetlands because of dispersal-limitation

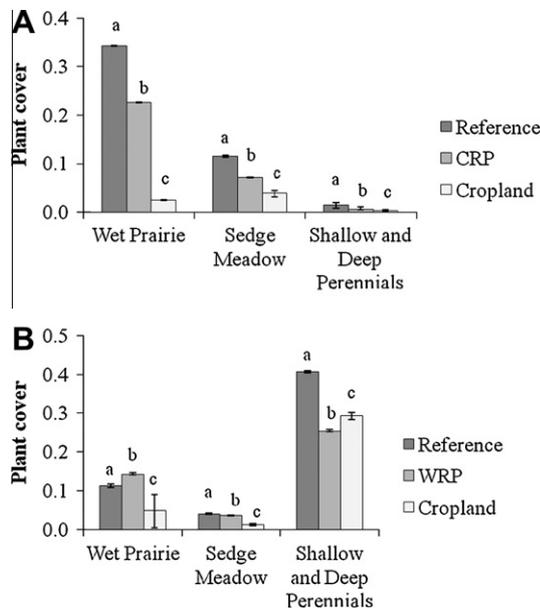
Within reference wetlands, species composition varied with all canonical axes, suggesting landscape isolation metrics were correlated with composition in both the WHP and RWB (WHP:  $F = 3.102$ ,  $P < 0.001$ ; RWB:  $F = 2.038$ ,  $P < 0.001$ ). In the WHP, distance to reference and playa area within 15 km were the best predictors of composition (Fig. 5a). Unlike results for perennial species richness in the RWB, both distance to reference and area of playas within 5 km were the best predictors of species



**Fig. 2.** pCCA of plant community composition (proportion of total cover) among land-use in the (A) WHP and (B) the RWB. Species are indicated by the first four letters of genus and species. Symbols indicate guild classification.

composition (Fig. 6a). Dispersal-limited plants had lower cover in isolated CRP or WRP playas and greater cover in clustered playas, while the converse was true for cosmopolitan plants ( $P < 0.001$  for all model effects in both regions; Figs. 5b and 6b; in the WHP, per-

cent deviance explained for dispersal limited plants was 35% and was 5% for cosmopolitan species; in the RWB, percent deviance explained for dispersal limited plants was 28% and was 10% for cosmopolitan species).



**Fig. 3.** Wetland perennial guild cover in playas among land-use in (A) the WHP and (B) RWB. Lowercase letters indicate significant differences ( $P < 0.05$ ) in plant cover between land-use types.

**4. Discussion**

Cover of perennial wetland guilds was far less in non-reference land-uses and related to landscape isolation metrics, supporting the dispersal-life history wetland plant model. In the RWB, cover of perennials guilds with high inundation tolerance differed by land-use, e.g. sedge meadow and shallow and deep emergents, but not wet prairie perennials, which tolerate somewhat wet to dry conditions. However, precipitation is greater in the RWB than in the WHP. Therefore, the landscape matrix likely was more suitable for wet prairie plants in the RWB than in the WHP, reducing dispersal distances into previous croplands. Perennials requiring inundation to regenerate may have been most dispersal-limited

because inundated wetlands were rarer on the landscape than dry wetlands (O'Connell et al., 2012). Thus conditions for species presence were twofold. First, propagules must reach the site (dispersal-limitation) or be present in the seed bank (relationship with dispersal discussed below). Second, conditions for establishment must be present (environmental conditions).

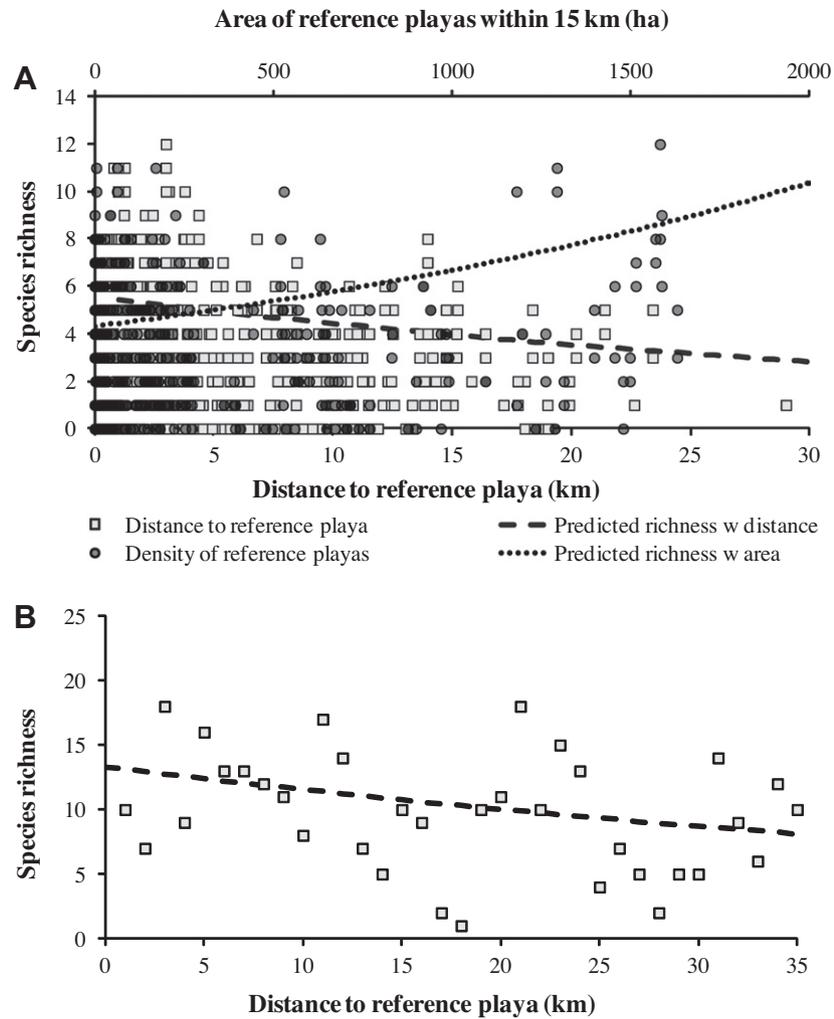
Reduced perennials in cropland playas probably was explained by reduced perennial seed banks. Cropland wetlands in the WHP have shorter hydroperiods than reference wetlands and are plowed during dry years (Tsai et al., 2007). Both shorter hydroperiods and plowing may reduce perennial seed production. For example, plowing can remove extant perennials before they reseed (O'Connell, 2011). Shorter hydroperiods may kill perennials intolerant of dry conditions before reseeding. Some (though not all) perennials produce fewer seeds each season than annuals and are less disturbance tolerant (Shipley and Parent, 1991). Cropland reduction of perennial reproduction has been documented (Haukos and Smith, 1993; Galatowitsch and van der Valk, 1996). In the RWB, both extant vegetation and seeds of perennial species were lower in croplands and WRP than in reference playas (Beas, 2011). Reduced perennial seed banks lessen perennial cover after cultivation ceases, again, unless perennials recolonize from nearby wetlands.

Additionally, we identified an inverse relationship between landscape isolation and perennial wetland richness. Importantly, these models incorporated some environmental factors related to germination and disturbance, such as playa inundation and land-use. This means that landscape isolation metrics explain perennial species richness after accounting for variation due to these factors. Landscape isolation did not interact with land-use, suggesting isolation was important across all land-uses. In the RWB, only distance was important, whereas in the WHP both distance and surrounding playa area explained richness. Playas in the WHP were smaller and drier than those in the RWB (Smith, 2003). Thus in the RWB, a nearby reference playa alone may be an adequate propagule source because playas are large and regularly inundated. In the WHP, a single small reference playa may not be an adequate source because it may often be dry and not contain enough individuals to sustain populations. Haukos and Smith (2004) showed

**Table 1**

Species richness of wetland perennials in the WHP and the RWB. CI is the parameter 95% confidence interval. Models have Poisson error distribution and log-link between model and response. The null model was not among models with  $\Delta AIC < 4$ . Parameter importance (number of models in which variable was selected divided by total possible models) is indicated. The parameter land-use and land-use \* area interactions appeared for both WHP and RWB models.

	Parameter	Coefficient	Lower CI	Upper CI	Importance
WHP	Reference				
	Intercept	0.2544	0.0841	0.4236	1
	Distance to reference playa (km)	-0.0224	-0.0339	-0.0108	1
	Playa inundated	0.1800	0.0659	0.2950	0.89
	Playa area (ha) w/in 15 km	0.0004	0.0003	0.0006	1
	CRP				
	Intercept	1.1530	0.8190	1.4870	1
	Distance to reference playa (km)	-0.0224	-0.0339	-0.0108	1
	Playa inundated	0.1800	0.0659	0.2950	0.89
	Playa area (ha) w/in 15 km	0.0004	0.0003	0.0006	1
	Cropland				
	Intercept	0.2720	0.1060	0.4370	1
Surveyed area (ha)	0.0204	0.0167	0.0242	1	
Distance to reference playa (km)	-0.0224	-0.0339	-0.0108	1	
Playa inundated	0.1800	0.0659	0.2950	0.89	
Playa area (ha) w/in 15 km	0.0004	0.0003	0.0006	1	
RWB	Reference				
	Intercept	2.4500	1.8880	3.0000	1
	Distance to reference playa (km)	-0.0142	-0.0264	-0.0021	0.96
	WRP				
	Intercept	2.1810	1.6010	2.7500	1
	Distance to reference playa (km)	-0.0142	-0.0264	-0.0021	0.96
	Cropland				
	Intercept	1.2900	1.0100	1.5600	1
	Surveyed area (ha)	0.0052	0.0033	0.0071	1
	Distance to reference playa (km)	-0.0142	-0.0264	-0.0021	0.96



**Fig. 4.** Richness of wetland perennials and landscape isolation metrics in (A) the WHP and (B) RWB. Prediction line is in the units of the data and indicates an inundated reference playa with other variables in model (Table 1) held at their mean.

**Table 2**  
Wetland annual plant species richness in the WHP and the RWB. CI is the parameter 95% confidence interval. Models have Poisson error distribution and log-link between model and response. The null model was not among models with  $\Delta AIC < 4$ . Parameter importance (number of models in which variable was selected divided by total possible models) is indicated. The parameter land-use and land-use \* area interactions appeared in all models.

	Parameter	Estimate	Lower CI	Upper CI	Importance
WHP Reference	Intercept	1.4759	1.2507	1.7001	1
	Playa inundated	0.3275	0.2359	0.4191	1
	Playa area (ha) w/in 5 km	0.0013	0.0004	0.0022	1
CRP	Intercept	1.4742	1.2453	1.7022	1
	Playa inundated	0.3275	0.2359	0.4191	1
	Playa area (ha) w/in 5 km	0.0013	0.0004	0.0022	1
Cropland	Intercept	1.0060	0.9024	1.1087	1
	Surveyed area (ha)	0.0161	0.0129	0.0192	1
	Playa inundated	0.3275	0.2359	0.4191	1
	Playa area (ha) w/in 5 km	0.0013	0.0004	0.0022	1
RWB Reference	Intercept	1.8605	1.4009	2.3196	1
	Surveyed area (ha)	0.0012	0.00004	0.00242	1
WRP	Intercept	1.9760	1.4969	2.4547	1
	Surveyed area (ha)	0.0012	0.00004	0.00242	1
Cropland	Intercept	1.5470	1.3157	1.7779	1
	Surveyed area (ha)	0.0012	0.00004	0.0024	1

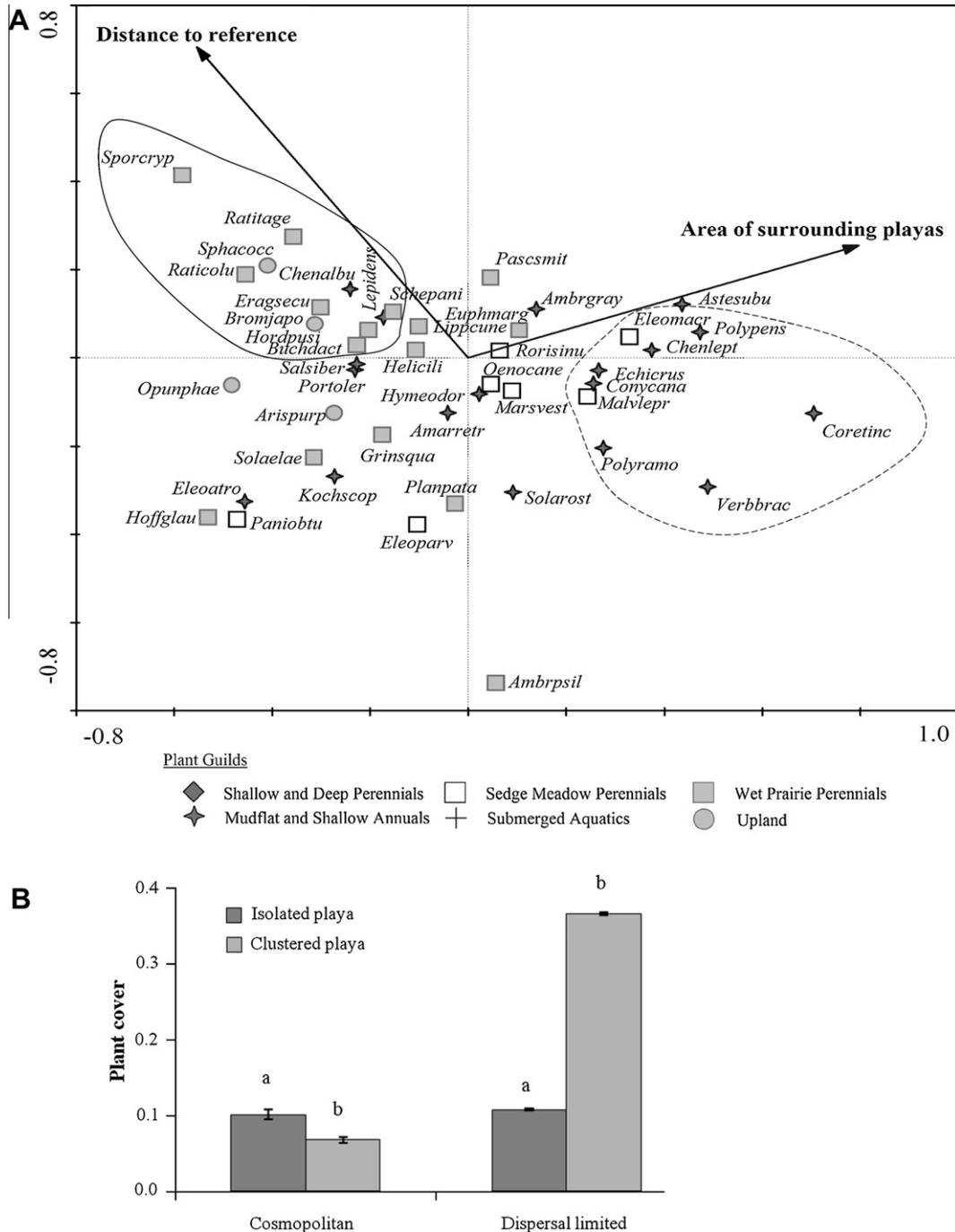
**Table 3**

Explained deviance for models containing all candidate predictors for wetland annual and perennial species richness. Wetland perennial and annual means ( $\bar{x}$ ) also are provided.

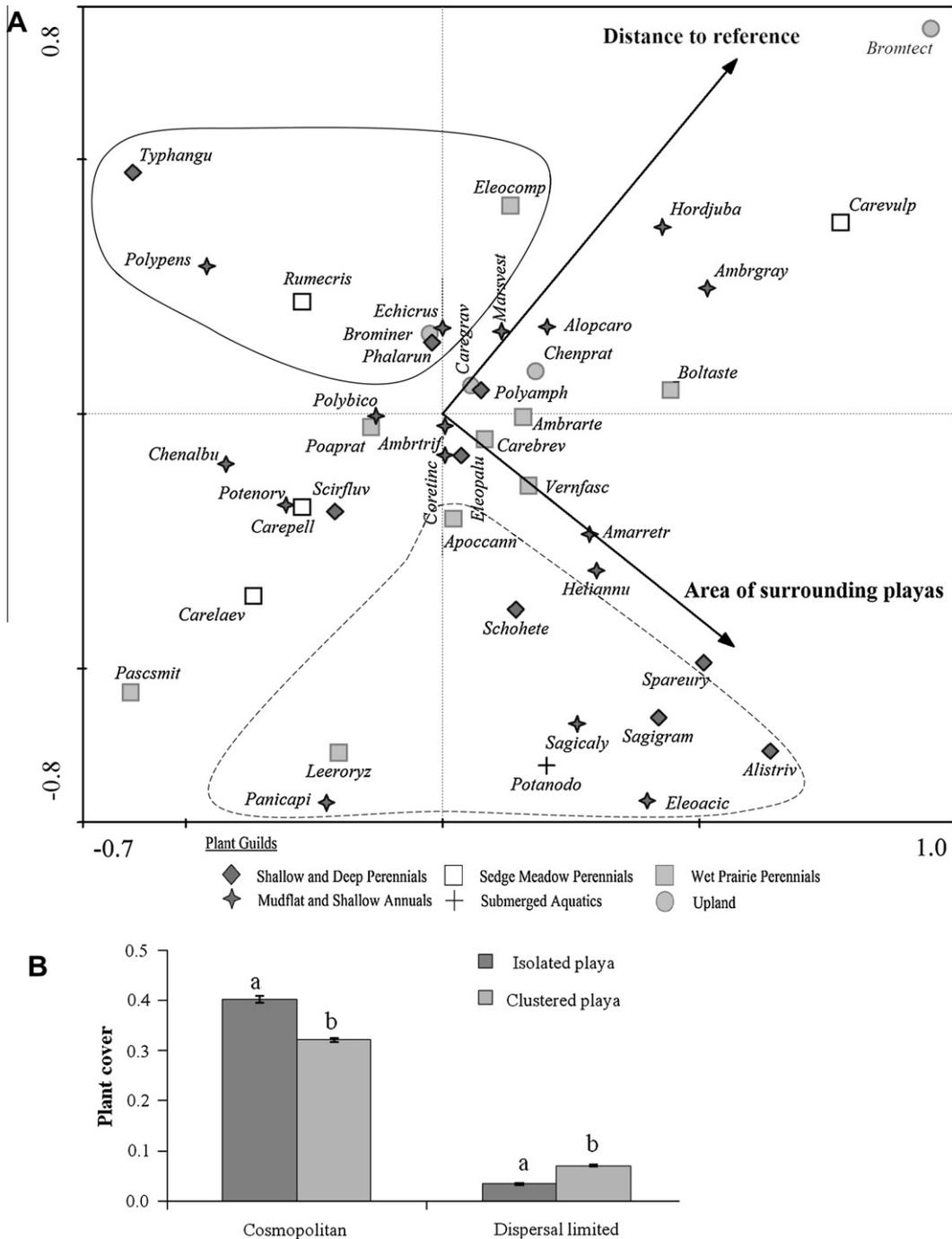
	WHP		RWB	
	Perennial	Annual	Perennial	Annual
Explained deviance	40.4	21.6	45.1	38.3
Reference	$\bar{x} = 5.0$	$\bar{x} = 5.4$	$\bar{x} = 13.0$	$\bar{x} = 8.1$
Previous cropland	$\bar{x} = 3.5$	$\bar{x} = 5.2$	$\bar{x} = 10.1$	$\bar{x} = 8.2$

species richness increased with surrounding playa numbers in the Southern High Plains. Further, cultivation progressively removes cropland playas in WHP because they infill with upland sediments (Luo et al., 1997). Half of the WHP has been converted to cropland, thus likely increasing dispersal distances between playas.

Dispersal distances for species likely varied with dispersal vectors (Ozinga et al., 2009). In isolated wetlands, direct water dispersal between wetlands should be rare because water connections between wetlands are lacking. Animals also are



**Fig. 5.** (A) pCCA of plant composition (proportion of total cover) in reference playas, with distance to reference playa and surrounding playa area within 15 km, in the WHP. Dashed and solid lines encircle dispersal-limited and cosmopolitan species respectively. (B) Plant cover for cosmopolitan and dispersal-limited plants in clustered and isolated CRP playas.



**Fig. 6.** (A) pCCA of plant community composition (proportion of total cover) in reference playas, with distance to reference playa and area of surrounding playas within 5 km in the RWB. Dashed and solid lines encircle dispersal-limited and cosmopolitan species respectively. (B) Plant cover of cosmopolitan and dispersal-limited plants in clustered and isolated WRP playas.

dispersal agents and disperse seeds of preferred food types (Chang et al., 2005). Thus waterfowl disperse mainly annual seeds, whereas small mammal herbivores may disperse moderately water tolerant perennials (Chang et al., 2005). Wind and animal dispersal probably were common. Seeds also may be dispersed by multiple events. For example, wind might carry wetland seeds into the upland of an adjacent catchment. Subsequent precipitation might wash those seeds into the adjacent wetland basin. Frequency and distance of dispersal by various mechanisms has not been examined here, but see Ozinga et al. (2009).

In contrast to perennial species, wetland annual species had equivalent richness in reference and previous cropland wetlands.

Landscape isolation models explained less variation in annual species richness than those for perennial species richness, though surrounding playa area still was influential in the WHP. Landscape isolation may influence annual species less either because cropland activities increase spatial evenness of annual species or because annuals produce greater seeds and have more dispersal events. Therefore, we should evaluate influences of landscape isolation on individual species as well as species groups when making planting decisions.

Altogether, our results imply many perennial wetland species were dispersal-limited, causing decreased cover of perennials in wetlands where past agriculture reduced perennials. Wetland

perennials were also dispersal-limited in prairie potholes (Mulhouse and Galatowitsch, 2003; Galatowitsch, 2006). Further, Ozinga et al. (2005) suggested many plants do not occupy their theoretical niche because of dispersal barriers. Thus, there is evidence that dispersal-limitation is an important constraint on plant assembly.

#### 4.1. Applying analytical approaches to aid restoration

Dispersal-limitation observed in reference conditions explained communities in previously-cropped wetlands. Restoration managers might use analyses of plant communities in reference sites as tools informing restoration practices. This process is summarized in Fig. 7. For example, our model predicts that in the RWB, isolated unplanted WRP wetlands should develop high cover of *Typha angustifolia* (cattail), *Phalaris arundinacea* (reed-canary grass), *Polygonum pensylvanicum* (pink smartweed), *Echinochloa crus-galli* (barnyard grass), as well as other species encircled by the solid line in Fig. 6a. If wetlands with plant cover dominated by these species meet management goals, then planting is unnecessary.

It is worth noting that while some cosmopolitan species were not annuals, they all were disturbance tolerant and some (e.g., *P. arundinacea*) were nuisance species in the RWB. The spread of nuisance species is sometimes reduced by planting with desirable species (Lodge, 1993). Indeed, *P. arundinacea*, highly invasive in wetlands, sometimes has reduced occurrence in habitats with high species richness (Lavergne and Molofsky, 2004). Ordination techniques are useful for informing restoration decisions because they

depict landscape relationships for individual species. While we argue perennial wetland plants in general are dispersal-limited, individual species, such as *T. angustifolia*, may differ, with important restoration consequences.

Thus, whether to plant new restorations depends on targeted plant communities and landscape position of restored wetlands. If communities containing mostly cosmopolitan plants as defined by ordination are not acceptable, then the restoration should be planted if it is more than the mean distance away from reference wetlands or has less than average area of reference wetlands in the surrounding landscape (Fig. 7). Appropriate metrics determining landscape isolation in plants can be identified using model selection techniques described in this paper. While our study in prairie landscapes with few rivers suggests how plants might behave, factors important elsewhere, such as distance to water dispersal vectors, can be incorporated as potential predictors into other regional models to inform planting decisions.

Our analysis makes specific restoration recommendations. Ordination depicts plant-landscape relationships on the scale of the data used in the region analyzed. Lengths of the landscape vectors displayed in pCCA are scaled to the landscape data generating the model. In the WHP, restored wetlands with >250 ha of surrounding reference wetlands within 15 km and <2 km to nearby reference wetlands should not require planting of dispersal-limited species. Similarly, in the RWB, clustered wetlands are those with >1500 ha of reference wetlands within 5 km and <1.5 km of nearby reference wetlands. Analyses of this kind can be used to make similar recommendations for plant species observed elsewhere.

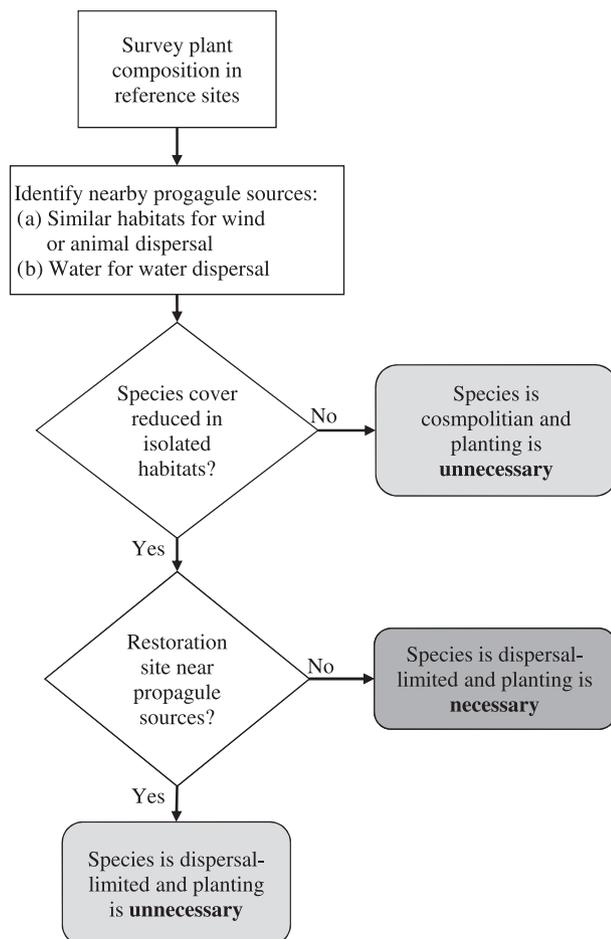


Fig. 7. Diagrammatic process for making wetland planting decisions at restoration sites in novel study areas.

#### 4.2. Model limitations and conclusions

We hope our model may be generally applicable and can be incorporated into larger restoration efforts. We encourage further analyses in other regions to verify our suggestions. Further, all models have assumptions and limitations. Extant plant composition in reference wetlands is only informative if unmeasured factors were not confounding. Confounding factors may include soil nutrients such as nitrogen and phosphorus, which influence colonization and competition. We have data suggesting total soil nitrogen did not differ by land-use in the WHP, though individual nitrogen species may (O'Connell, unpublished data). Phosphorus was similar between reference and cropland playas, but differs for CRP playas (Beas, unpublished data). Similarly, in the RWB, phosphorus was similar in all land-uses, but data on nitrogen were lacking (Beas, unpublished data).

Likewise, hydrology influences wetland plants. Playa inundation was similar among land-use types in the RWB (O'Connell, 2011). However, in the WHP, CRP playas inundated less than reference and cropland, probably due to introduced tall-grass cover (Cariveau et al., 2011; O'Connell et al., 2012).

Further time since restoration relates to plant community composition. Our previously cropped wetlands were removed from production 1–20 years prior to surveys. Wetland perennial species also were underrepresented in prairie potholes 12 years post-restoration (Galatowitsch, 2006). We do not know if underrepresented perennials will establish, but we suggest planting may be optimal when timescales >10 years do not meet management goals.

We should consider confounding factors while planning restoration. While we concentrated on plant life history and landscape isolation influences on restoration success, we do not suggest these are the only important restoration factors. Rather, we hope these analyses augment toolsets of restoration managers, increasing restoration success and protecting biodiversity.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2012.10.019>.

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