MAPPING, HYDROLOGIC MODELING AND

CONNECTIVITY OF DEPRESSIONAL WETLANDS IN

CENTRAL OKLAHOMA

By

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Title of Study: MAPPING, HYDROLOGIC MODELING AND CONNECTIVITY OF
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Abstract: The objectives of this study were to (1) develop a method to improve map quality for temporarily inundated depressional wetlands in central Oklahoma, (2) create a predictive hydrologic model for those wetlands, and (3) assess the spatiotemporal variability in landscape connectivity on invertebrate communities.

(1) Accurate wetland maps are an important resource for wetland management with applications including prioritizing restoration and tracking habitat loss. Traditional wetland maps utilize single-date imagery often underestimating ephemeral wetlands. High-recurrence satellite imagery was classified to identify patterns of inundation in regional wetlands over an 18 year period with high accuracy. Updated maps identified over 700 more wetlands than maps previously available for the area. Because new maps were created using long-term inundation information, they also included more accurate water regime attributes.

(2) Classified satellite images were also used to develop regional wetland hydrologic models. Inundation in approximately 500 wetlands was modeled over 18 years using climate data, land-use and wetland size as independent variables. The quantity, intensity and timing of rainfall as well as long-term drought indices were all important in predicting wetland inundation. Furthermore, small wetlands in grassland watersheds were less likely to be inundated than large wetlands surrounded by agriculture. Under future climate scenarios, regional wetlands are potentially at risk of decreased frequency of inundation, with small grassland wetlands most vulnerable.

(3) Landscape connectivity of inundated wetlands also impacts biotic communities. This study provides evidence for temporally variable effects of connectivity and vegetation complexity on wetland invertebrate richness and metacommunity organization. Late in the growing season vegetation complexity had a greater effect on richness and sites with similar vegetation increased in community similarity. Permanent wetlands appear to act as refuges during periods of drought and supply colonists to temporary wetlands early in the growing season. Early in the season dispersal increases wetland richness and makes proximate sites more compositionally similar. Late in the season, the spatial scale at which wetlands are connected appears to depend on the number of inundated wetlands regionally. Understanding the temporal fluctuations in local and regional effects is likely to elucidate the complex patterns of wetland invertebrate community organization.

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CHAPTER I

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MAPPING AND HYDROLOGIC ATTRIBUTION OF TEMPORARY WETLANDS USING

RECURRENT LANDSAT IMAGERY

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Abstract: In areas with a high density of ephemeral wetlands, traditional mapping protocols may underestimate occurrence of wetlands when single-date base-imagery is utilized. In the Pleistocene Sand Dunes Ecoregion in Oklahoma, National Wetland Inventory (NWI) maps created using base-imagery from a dry year omitted large numbers of ephemeral wetlands. To improve the likelihood of capturing inundated depressions, we classified water pixels from 51 Landsat images (3 images per year: pre/early, peak, and late/post growing season) from 1994-2011. Several image classification methods were tested but decision tree analysis with training pixels from multi-season imagery provided the greatest accuracy. Accuracy was determined through manual comparison of two Landsat images with concurrent aerial imagery (Kappa =0.96 and 0.93 for the two images). Wetland polygons were created from water/non-water rasters and given hydroperiod designations based on the number of inundated periods. Landsat-derived wetland maps identified 3,156 wetland units, 718 more than the original 1980s NWI, with only 33.9% agreement between the two maps. Finally, one meter LiDAR data were combined with classified Landsat images to determine the volume of water in wetlands during each image date. These wetland maps can assist with estimating the availability of inundated habitat during wet, dry, and average rainfall periods.

INTRODUCTION

Accurate wetland maps are an invaluable resource for wetland monitoring and management, with applications including tracking wetland loss and gain and prioritizing restoration sites. The National Wetlands Inventory (NWI) is the most extensive and detailed wetland map for most of the conterminous United States. Much of the United States, including the majority of Oklahoma, was mapped in the 1980s predominantly from single-date 1:58,000 color-infrared imagery (USFWS 2014). Single-date imagery can be problematic for identifying wetlands that are only distinguishable from surrounding uplands for portions of the year. For example, evaluations of NWI maps have demonstrated that accuracy can be reduced in densely forested landscapes (Stolt and Baker 1995; Tiner 1997; Brooks et al. 1999; Kudray and Gale 2000). Additionally, regions with temporary or seasonal depressional wetlands are also susceptible to errors of omission using single-date imagery (Martin et al. 2012). Observed from above, these depressions often appear identical to the surrounding uplands when dry and/or farmed.

In the Central Great Plains and Cross Timbers Ecoregions of Oklahoma, Dvorett et al. (2012) found that over 30% of NWI polygons were uplands, lost since map creation over 30 years ago, or attributed with an incorrect hydroperiod. In Oklahoma, the need for more accurate maps is critical as the state currently uses NWI maps for preliminary wetland determinations and project planning, identifying suitable restoration sites to reduce non-point source pollution to impaired waterbodies (OCC 2013), and tracking wetland loss and gain in accordance with no-net loss (OCC and OWRB 2010, OCC and OWTWG 2012). NWI map accuracy appears to be particularly poor in the Pleistocene Sand Dunes Ecoregions that have formed primarily on the leeward terraces of several large rivers including the Cimarron, North Canadian, and Salt Fork of the Arkansas Rivers. In these regions, wetlands occur in high density in the valleys between dunes, and inundation periods are often temporary (Lepper and Scott 2005). Additionally, depressions may be dry for several consecutive

years due to variable rainfall patterns in the semi-arid Central Great Plains. The erratic interdunal inundation pattern makes wetlands susceptible to omission from single-date mapping.

Supplementing traditional single-date mapping with high-recurrence satellite imagery has the potential to improve the identification of wetlands in areas that contain high densities of temporary wetlands. Using multiple images from multiple years, it is possible to estimate the frequency and duration of inundation of each depression. This allows not only for increased detection of wetland basins, but improved hydrologic attribution of wetland polygons (Beeri and Phillips 2007; Rover et al. 2011; Collins et al. 2014). Of the NWI attributes, the water regime modifier has been one of the most difficult to accurately apply to wetland polygons during mapping (Graves 1991; Cowardin and Golet 1995; Dvorett et al. 2012). Determining water permanence can be extremely difficult using single-date imagery but should be improved by utilizing several images from the same year, for multiple years.

The Landsat project, a joint initiative between the U.S. Geological Survey (USGS) and National Aeronautics and Space Administration (NASA), has been continuously acquiring satellite data of the Earth's surface since 1973 (USGS 2013). The high return interval, multi-spectral bands, moderate spatial resolution, and free availability of Landsat data make it extremely useful in supplementing single-date wetland maps. Another advantage of utilizing multi-spectral satellite data in wetland mapping is that identification of wetlands can be automated through land-cover classification, for which a number of techniques and methods exist (Ozesmi and Bauer 2002). As a result, several studies have been conducted using several Landsat images to map wetlands (Lunetta and Balogh 1999; Frazier and Page 2000; Baker et al. 2006). However, in regions with a high density of temporary or intermittently flooded wetlands, the number of satellite images may need to be increased to accurately map wetlands. Others have used a large number of multi-season satellite images to better characterize the hydrologic attributes of previously mapped prairie depressional wetlands (Beeri and Phillips 2007; Rover et al. 2011; Collins et al. 2014). These same types of

approaches can also be applied to initially identify or map wetlands by filtering long-term, spatially-explicit hydrologic datasets with inundation thresholds sufficient for regional wetland formation.

With the wealth of freely available remotely sensed data, there is further potential for improved accuracy or additional attribution of wetland polygons. For example, relatively new technology such as Light Detection and Ranging (LiDAR), which measures distance by analyzing the light reflected off an object targeted with a laser, can provide extremely high resolution elevation data (Lillesand et al. 2015). Combining LiDAR-derived elevation data with Landsat-derived wetland inundation maps can provide information regarding the volume and depth of a wetland polygon. With the addition of three-dimensional hydrological measurements, such as volume, to wetland mapping, it is possible to estimate water storage and model related ecosystem services such as wildlife habitat as well as flood, nutrient or sediment reduction of downstream receiving water bodies (Huang et al. 2010; Lane and D'Amico 2010). Further, wetland managers can model the effects of wetland loss or climate change on regional hydrology and subsequent landscape services.

The objectives of this study were to (1) evaluate Landsat classification techniques for wetland identification and determine a regionally accurate method for the Pleistocene Sand Dunes Ecoregion of central Oklahoma, (2) combine Landsat classification data with single-date mapping to improve the accuracy of wetland identification and hydrologic attribution in the region, (3) further attribute wetland polygons with volume and depth measurements using LiDAR to improve regional wetland planning, and (4) provide guidance for future satellite-based wetland mapping efforts in other regions.

METHODS

Study Area

The study area is represented by the eastern portion of the Pleistocene Sand Dunes Level IV Ecoregion, north and east of the Cimarron River in central Oklahoma (Omernik 1987). The area includes portions of Logan, Kingfisher, Garfield, and Major counties, totaling approximately 1,300

km^2. In the region, aeolian dune formation and migration has occurred during episodic drought conditions on the leeward terraces of the Cimarron River. On the second quaternary terrace of the Cimarron River, the last period of significant deposition occurred approximately 800 to 900 years ago. When dunes stabilized, stream channels became blocked by dune emplacement and wetlands formed within interdunal valleys (Lepper and Scott 2005). Average rainfall for the region is approximately 83 cm in the east and 75 cm in the west. However, in the last 10 years, yearly rainfall in the eastern portion of the study area has ranged from 145 cm (2007) to 53 cm (2012). The average yearly potential evapotranspiration greatly exceeds average yearly rainfall in the region (Oklahoma Mesonet 2015).

Datasets

We included fifty-one Landsat 5 (LT5) and Landsat 7 (LE7) images from a single scene (Path 28 Row 35) in this study, with three images per year for an 18-year period from 1994 to 2011. A list of all the images used can be found in Table 1. Landsat images from each year were selected to represent pre/early growing season with a target date of 1 March, peak growing season with a target date of 1 July, and a late/post growing season with a target date of 15 October. Images diverged from target date based on the availability of images with less than 10% cloud cover and no "popcorn clouds" (isolated cumulus or stratocumulus clouds) (Collins et al. 2014). Because no cloud-free scenes were available for pre/early growing season in 1994, a scene from 4 December 1993 was used as a surrogate. All Landsat images were converted to surface reflectance using the Landscape Ecosystem Disturbance Adaptive Processing System (LEDAPS) atmospheric correction (Vermote et al. 1997, Masek et al. 2013).

LiDAR elevation data were generated by the USDA Natural Resources Conservation Service (NRCS) with 18.5 cm vertical accuracy and 1.4 m point spacing (NRCS 2012). LiDAR data were collected in January 2012 during a period of prolonged drought when most of the wetlands in the

study area were dry. It is impossible to confirm exactly how many wetlands had water during the time of LiDAR collection because Landsat 5 failed at the end of 2011. The last cloud free Landsat 5 scene from 20 October 2011 revealed that approximately 50 natural depressions (excluding river channels and impounded ponds) contained water. Rainfall from 20 October 2011 through January 2012 was roughly equivalent to average pan evaporation for the region and central Oklahoma was in extreme drought at the end of October 2011 (NOAA 1982; Oklahoma Mesonet 2015). As a result, we presume the elevation data represent the substrate of most natural depressional wetland basins rather than the water surface.

Image Classification and Accuracy Assessment

We selected at least 700 training pixels in each of five land-cover classes (crop, grassland, urban, forest, and water) from an LT5 image collected on 4 May 2008. A National Agricultural Imagery Program (NAIP) image, with 1 m spatial resolution, collected on the same date was used to identify the land-cover of Landsat pixels. Image classification was conducted in ENVI 5.2 (Exelis Visual Information Solutions, Boulder, Colorado). Methods included maximum likelihood, decision tree analysis, and manually determined thresholds for Landsat bands. Decision trees were created using the package rpart.plot (Milborrow 2011) in program R (R Core team 2013). Once maximum likelihood and decision tree classifications were complete, all upland classes were grouped together, thus classified images only contained water and upland pixels. We identified manually-determined breakpoints to separate water and upland pixels using Band 5 (B5) as well as Band 5 minus Band 3 (B5minB3) classifications (Lunetta and Balogh 1999; Collins et al. 2014). Accuracy assessments of the initial classifications were conducted by randomly selecting 200 water pixels and 1,000 upland pixels and comparing the Landsat classification to the concurrently collected NAIP image. A Landsat water pixel was deemed correct if it contained at least 25% water pixels in the concurrent NAIP image. We selected a low threshold for correct inclusion in the water class (25%) because the goal was to develop a classification that minimized errors of omission and maximized identification of

water pixels given the small size of many wetlands in the region. For each classification, we calculated confusion matrix elements: User's Accuracy (a measurement of errors of commission or false positives), Producer's Accuracy (a measurement of errors of omission or false negatives), and Kappa statistic. Kappa ranges from 0 to 1 and compares the observed accuracy to the expected accuracy of a random classifier given the confusion matrix. A kappa greater than 0.80 is generally considered excellent (Landis and Koch 1977).

When classifications were applied to Landsat images from other seasons, misclassification arose due to the changing spectral signatures of land-cover. Because no high resolution aerial photography is available from other periods of the year to compare with classified Landsat scenes, misclassification was assessed based on visual inspection of the imagery and knowledge of the region. As a result, we increased the training pixel pool to include locations for all upland classes from four Landsat images from 2008 (1 March, 4 May, 23 July, and 27 October). Our assumption was that land cover did not change through 2008 on upland pixels selected from the 4 May NAIP image. We then reran the decision tree analysis with the increased pool of training pixels. Accuracy assessments were again conducted by comparing 4 May 2008 NAIP and LT5 images. An additional accuracy assessment was also conducted by comparing LE7 imagery collected on 2 May 2010 with NAIP imagery collected on 5 May 2010. No rain occurred in the region between the dates of 2 May and 5 May, which allows for an accurate comparison between the water pixels present in the NAIP and Landsat images. We then applied the decision tree based on multi-season training data to the remainder of the Landsat scenes to identify water pixels in all 51 images.

Huang et al. (2014) found that LEDAPS atmospheric correction was incomplete for mapping wetland inundation and change in the Coastal Plain of the Chesapeake Bay Watershed of Delaware and Maryland, USA. Therefore, we assessed if LEDAPS could be improved by using the radiometric normalization method, iteratively re-weighted multivariate alteration detection (IR-MAD) (Canty and Nielsen 2008). IR-MAD uses an automated approach to identify "no-change pixels", which can then

be used to normalize an image to a reference. The 4 May 2008 image was used as a reference to normalize the 2 May 2010 image. We applied the final decision tree classification to the 2 May 2010 Landsat image before and after radiometric normalization to determine if accuracy was improved after normalization. All pixels within a 380 km^2 subset that changed classes after normalization were compared to the concurrent NAIP image to determine if normalization improved classification accuracy.

Map Creation

We created final wetland maps in ArcMap 10.1 (ESRI, Redlands, California) after all Landsat images were classified using decision tree analysis with multi-season training data. A pixel was considered a wetland pixel if it was classified as water for at least 25% of the years that were included in this study (Tiner 1991). Because 25% of 18 years of data is 4.5 years, we rounded up and deemed a pixel a wetland if it was classified as water in five years. Pixels were attributed with frequency of inundation, average hydroperiod, NWI water regime, average volume, maximum volume, average depth, and maximum depth. Each pixel was assigned an average hydroperiod by summing the number of consecutive wet scenes for all years the pixel contained water and then dividing the sum by the total number of years a pixel contained water. Average hydroperiod values that initially ranged continuously from one to three were rescaled to a discrete scale of one to four according to the following: 1 (wet 1.0 to 1.5 images per year), 2 (1.6-2.5), 3 (2.5-2.9), and 4 (wet every image in every year the basin was inundated) (Beeri and Phillips 2007).

Each pixel was also assigned a frequency of inundation value of 10 (inundation in at least one scene 25-50% of years), 20 (51-80%), 30 (81-99%) and 40 (100%). Frequency and hydroperiod values were then summed, giving each pixel a value representing the frequency and duration of flooding. Scores ranged from 11 to 44. For example, a value of 22 represents a wetland that is inundated approximately 51-80% of years (frequency inundation score of 20) and, when wet, holds

water on average for half of the growing season or 2 consecutive Landsat scenes (average hydroperiod score of 2). We also applied traditional NWI water regime modifiers to polygons based on frequency and duration score as follows: temporary (11, 21, 31, and 41), seasonal (12, 13, 14, 22, 23, 24, 32, and 42), semi-permanent (33, 34, and 43) and permanent (44). The final wetland raster was converted to a shapefile and dissolved based on the water regime attribute in ArcMap 10.1 (ESRI, Redlands, California). "Dissolve" allows for the combination of polygons that share a boundary and/or an attribute.

Each depressional wetland basin was then attributed with maximum volume, average volume, maximum depth and average depth in ArcMap 10.1 (ESRI, Redlands, California). We converted the LiDAR dataset (NRCS 2012) to a triangulated irregular network (TIN). We then applied the surface volume tool to the final wetland polygons for each basin as well as the maximum extent of water for each basin during the study period to calculate average volume and maximum volume respectively. We calculated depth by applying the zonal statistics tool to determine the average, minimum and maximum elevation for each wetland polygon as well as for the greatest extent of water for each basin during the study period. Average depth was calculated by subtracting the average elevation within the wetland polygon from the maximum elevation. We calculated maximum depth by subtracting the minimum elevation within the greatest extent of water during the study from the maximum elevation.

To reduce errors of commission in the Landsat-derived wetland map, all wetlands that did not intersect manually digitized wetland polygons from 2008 base imagery were further inspected. When these polygons did not occur in a topographic depression or when the years they were inundated did not correspond with rainfall patterns, the polygons were removed from the final map. The topographic depression layer was developed by applying the depression evaluation tool to the LiDAR dataset (NRCS 2012) in ArcMap 10.1 (ESRI, Redlands, California).

In addition to developing a wetland map based on Landsat classification, we conducted traditional NWI mapping using 4 May 2008 NAIP imagery as the base image, following Federal Geographic Data Committee (FGDC) guidelines (FGDC 2009). We conducted both visual and automated quality control using the United States Fish and Wildlife Service (USFWS) Wetland Data Verification Toolset (Bergeson 2011) in ArcMap 10.1 (ESRI, Redlands, California). Imagery from 2008 was chosen because it was a relatively wet year in the study area, making it more likely to observe water present in depressional wetlands.

We assessed the agreement between the original 1980s NWI map, the newly digitized NWI map from 2008 imagery, and the Landsat-derived wetland polygons. All datasets (original 1980s NWI, updated NWI, and Landsat classified wetland map) were dissolved in ArcMap 10.1 (ESRI, Redlands, California) so that individual wetland basins were considered for comparison, rather than multiple adjacent polygons reflecting differences in wetland vegetation or hydrology in a single basin. A wetland basin was said to agree between mapping methods if the outcomes intersected. We did not consider differences in the boundaries between wetland units.

Field Verification

Once maps were completed, in spring 2015 we conducted field verification of wetlands. Field verification sites were grouped into three categories: only mapped in the 2008 manual mapping effort (manual), only mapped in the Landsat-derived maps (digital), and mapped using both methods (agree). Given the high percentage (> 99%) of the sites located on private lands, as well as the time and difficulty involved in gaining landowner access permission, we conducted a "windshield" survey from the road.   Thirty wetlands corresponding to each map type (manual, digital, and agree) that were within 50 m of a road were selected for field verification. At each wetland, we observed hydrologic indicators, wetland vegetation, and topography. If wetland vegetation or hydrologic indicators were present, the site was considered a wetland. This follows the goals of NWI to map

scientifically accepted wetlands rather than regulatory wetlands (Tiner 1993; National Research Council 1995; Tiner 1999). Sites that lacked wetland indicators (hydrology and vegetation) and did not exist in a topographic basin or were surrounded by unfarmed land were considered commission errors (false positives). If the site lacked hydrology indicators and wetland vegetation but it was farmed and existed in a topographic basin, it was deemed undeterminable. The variable inundation patterns of the interdunal wetlands, coupled with the native vegetation loss from planting crops, made it impossible to definitively conclude the presence of a wetland in farmed depressions. Sites that were not visible from the road or were impacted by new infrastructure (e.g. road, house, oil-well pad) installed since 2008 were also removed from the sample population.

RESULTS

Image Classification

The initial classification parameters and the results of the accuracy assessment for the upland/water classification using single image training data from 4 May 2008 can be found in Table 2. We observed the histograms of upland and water pixels to minimize misclassification of training pixels, and developed two different classifiers, (1) B5<0.130 and (2) B5minB3<0.065 for water pixels. The decision tree classified water pixels using Band 4 (B4) <0.210 and B5minB3<0.160. All classifications used with single date training data produced good results, with kappa ranging from 0.84 (for decision tree classification) to 0.93 (for B5minB3 classification).

When classifications developed from 4 May 2008 training data were applied to Landsat imagery from other seasons, errors of commission in the water class increased dramatically. Classifications based on B5 alone, as well as B5minB3, grouped a large number of early spring and late fall evergreen pixels with the water class. B5 classification also placed early spring crop pixels in the water class. As a result, we reran the decision tree analysis with training data from 3 additional 2008 images. The updated decision tree classified water using the following thresholds B4<0.22 and

B5minB3<0.06. However, upon visual inspection prior to accuracy assessment, we found many turbid water pixels were excluded from the water class. As a result, an additional node was added to the decision tree (Fig. 2). Turbid water tended to have extremely low values for B5minB3 (less than 0), but reflected more in B4 than the decision tree allowed for water pixels. Classifications using the new decision tree were extremely accurate, with kappa values of 0.96 and 0.93 for 4 May 2008 and 2 May 2010 Landsat data, respectively (Table 2). The calculated classification accuracy above is dependent on the spatial threshold used to determine correct classification during the accuracy assessment. We used a threshold of $\geq$25% water on the NAIP image to be considered water during validation. Kappa statistics were still excellent when the spatial criteria for inclusion in the water class was increased to 50% water (2008 Landsat kappa of 0.94 and 2010 Landsat kappa of 0.92) and decreased to 1% water (2008 Landsat kappa of 0.89 and 2010 Landsat kappa of 0.98). Visual inspection of spring and fall Landsat scenes, using the updated decision tree based on all season training data, demonstrated the elimination of the majority of the errors of commission in the water class from crop and evergreen pixels.

IR-MAD normalization (Canty and Nielsen 2008) did not improve the accuracy of the classification of the 2 May 2010 Landsat image. Thirty-nine water pixels in the un-normalized image were converted to upland after normalization and 93 upland pixels were converted to water. Sixty-seven percent of both the water pixels lost and the water pixels gained after normalization were, in fact, verified as water using the concurrent NAIP imagery. The pixels that changed classes primarily appeared to represent the fringes of wetlands, where mixed upland-water pixels occurred (95% of water pixels lost to normalization and 86% of water pixels gained through normalization). Because normalization did not improve classification, it was not applied to the Landsat scenes included in this study.

Map Creation

The wetland map created through Landsat classification identified 3,156 total wetland units within the study area, or 718 more wetland units than the original 1980s NWI identified for the region. Agreement between the Landsat wetland map and the original 1980s NWI map was poor, with only 33.9% of Landsat wetlands mapped included in the original 1980s NWI. Agreement of Landsat maps was much greater with the manual NWI map created from 2008 base imagery. Overall, 81.3% of Landsat wetlands were identified in the 2008 NWI. Agreement increased as wetland size increased, with 95.3% of Landsat wetlands > 1.98 ha mapped from the 2008 base imagery. A summary of the agreement between wetland layers can be found in Table 3.

We identified 6,073 individual wetland units through manual mapping protocols using 2008 base imagery. Updated manual mapping identified significantly more wetland units than both Landsat classification and the original 1980s NWI maps. Agreement with Landsat maps was particularly poor for wetlands < 0.54 ha (22%), but improved dramatically for wetlands > 1.98 ha (84.6% agreement). The updated NWI diverged greatly from the original 1980s NWI maps, with an overall agreement of 25.2% and agreement for basins > 1.98 ha of 55.1% (Table 3). Not only did the original 1980s NWI fail to map a large number of wetlands identified through Landsat classification and updated manual mapping, but 36.5% of the original 1980s NWI units were unmapped by either Landsat classification or mapping using updated base imagery. An aerial image of a portion of the study area displaying the original 1980s NWI map, the 2008 base layer manual map, and the Landsat-derived map can be found in Figure 3.

Field Verification

Overall accuracy for manual, digital, and agree polygons was 91.67% (22 out of 24 sites), 87.5% (14 out of 16 sites) and 100% (23 out of 23 sites), respectively (Table 4). Four sites were removed because they were not visible from the road. Three sites were removed because they had

been lost to development since 2008 (two to oil well-pads and one to home construction). Twenty sites were deemed undeterminable because they lacked hydrologic indicators and hydrophytic vegetation but existed in farmed topographic basins.

DISCUSSION

In regions with large aggregations of ephemeral wetlands, single-date mapping can be particularly problematic. Original NWI mapping in the region was primarily completed using 1981 aerial imagery (USFWS 2014), which was a particularly dry year in central Oklahoma (Oklahoma Mesonet 2015). Furthermore, the relatively coarse scale (1:58,000) of the original 1980s NWI makes the detection of small depressional wetlands difficult. Simply using higher resolution NAIP imagery (1 m) from a wet year increased the detection of small ephemeral wetlands greatly. Although the newer NAIP images used for updated mapping were true-color and not color-infrared like the original 1980s NWI, the improved spatial resolution in a wet year more than compensated for the loss of the infrared spectral band.

Integrating multi-season, multi-year satellite data into traditional NWI mapping has the potential to improve the accuracy of wetland maps further in areas where wetland signatures are often difficult to identify. In the Pleistocene Dune Ecoregion, Landsat-derived wetland maps identified over 600 unique wetland polygons not included in the updated manual mapping effort and provided more detailed hydrologic information on the frequency and duration of inundation. Landsat-derived wetland maps were also a significant improvement on the original 1980s NWI maps. This is not an indictment of NWI, which still stands today as a major accomplishment, but rather a testament to the need for updating maps in problem areas, especially given the availability of newer data sources and knowledge of region-specific wetlands.

Map Accuracy and Field Verification

The original 1980s NWI maps for the Pleistocene Sand Dunes Ecoregion north of the Cimarron River in Oklahoma only included 35% of the wetland mapped using Landsat classification. Low commission error rates for Landsat-derived polygons provide evidence that these wetlands are real landscape features that single-date NWI mapping omitted. Field verification found error rates of 12.5% for polygons mapped using Landsat but not in manual maps. Polygons identified in both Landsat-derived and manual maps had a 0% error rate. Baker et al. (2006) also found relatively high accuracy (overall accuracy of 86% and Kappa of 0.788) using decision tree models to classify wetlands and riparian areas using multi-season LE7 imagery for the Gallatin Valley of southwest Montana.

While error rates were low in our study, single-visit field verification of temporarily flooded wetlands in farmed landscapes can be difficult. We could not definitively determine if 22.2% of the sites were wetlands or uplands. Hydrologic indicators have the potential to be absent during a site visit as a result of the temporary nature of inundation coupled with frequent periods of multi-year droughts. Tiner (1997) acknowledged that wetlands with "drier-end" hydrology are potentially problematic for both wetland mapping and delineation. Farming can make it even more difficult to identify wetlands, as plowing and planting removes the native plant community, and can remove hydric indicators from the soil (Hurt and Carlisle 2001). Tiner (1997) stated that NWI maps omitted many farmed wetlands by design because of the difficulty of identification. As NWI maps are updated in agricultural areas for regional wetland planning efforts, it is important that the abundance of farmed wetlands are included in final maps, so the resource can be effectively managed. Using multi-year, multi-season classified Landsat images may in fact be more reliable in identifying temporary and/or farmed wetlands than single-visit field verification. Upland commission errors in the Landsat image-derived water class were extremely low (1.5-6.5%), meaning a pixel mapped as water is likely to be water. Requiring individual pixels to be classified as water in multiple images

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reduces the risk that erroneous pixels are included in the final map. This does not guarantee that a site contains wetland characteristics, but rather it is extremely likely that it ponds water. As a result, future work to establish empirically derived regional hydrologic thresholds for the development of wetland characteristics may be more beneficial in creating accurate maps than single-visit field verification in landscapes dominated by farmed temporary wetlands.

Strengths and Limitations of Landsat Mapping

Once protocols are established, Landsat classification can generate wetland maps for a region much more quickly than manual polygon digitization. However, until high recurrence satellite imagery with high spatial resolution (~1 m) is freely available, satellite classification is unlikely to completely supplant manual wetland digitization from aerial-based imagery. In order to meet the NWI mapping standard of 98% inclusion of wetlands > 0.2 ha, Landsat-derived wetland maps will likely need to be integrated with manual maps. The 30-m resolution Landsat image failed to identify many small wetlands that had been digitized through manual mapping using wet-year base imagery; the 2008 wet-year manual wetland map identified 3,680 unique wetlands < 0.54 ha and 91% more wetlands <0.54 than the Landsat-derived map. However, Landsat-derived wetland maps agreed with the 2008 wet-year manual NWI on more basins in the 0.18 ha to 0.54 ha range than the original 1980s NWI. Only in the size class from 0.01 ha to 0.18 ha did the original 1980s NWI identify more of the 2008 NWI basins than Landsat maps. This is not surprising, given that a 0.18 ha wetland consists of two 900 m^2 Landsat pixels. Small basins generally consist of mixed pixels at the edge of wetlands that include both upland and wetland. The majority of omission errors from the water class in all classification methods developed for this study resulted from mixed upland/water pixels at the edge of wetlands. As a result, classifiers developed to separate water and upland pixels are more likely to miss small basins if they consist entirely of mixed pixels. Due to the spatial resolution of Landsat and the potential irregular shape of wetlands, FGDC (1992) suggests that it takes at least 9 pixels (0.9 ha) and as many as 25 pixels to consistently identify an object.

While Landsat-derived wetland mapping has shortcomings in identifying small wetlands, simply updating NWI by manually digitizing wetlands using newer wet-year imagery can lead to the inclusion of briefly inundated uplands in wetland maps. Using Landsat-derived wetland maps as a starting point for manual mapping would both expedite digitization and provide additional hydrological information for wetland inclusion. Areas that appear to be wetlands on wet-year base imagery, but were unmapped through Landsat classification, could be scrutinized further by observing the frequency and duration of inundation. Subsequent field visits to questionable manually mapped wetlands can be implemented to refine Landsat-derived hydrologic decision criteria (e.g. >25% wet years) for inclusion in wetland maps. While the Landsat maps would likely be of limited use for screening small wetlands (<0.4 ha), the detailed hydrologic data could be an effective screening tool for larger wetlands. Larger wetlands may have been missed during Landsat classification due to some sites lacking surface water (e.g., riparian areas), containing dense vegetation with little standing water, or having irregular shape (mixed upland/wetland pixels) (Park et al. 1993; Hinson et al. 1994; Ozesmi and Bauer 2002). Other areas of standing water on wet-year imagery may not be wetlands (e.g., sheetwater in agricultural fields), and they can be filtered out of the final maps by observing long-term Landsat hydrological data. There are additional potential problems using only single-date wet-year imagery for mapping, such as the variable nature of the rainfall in the region, even in wet years, causing localized regions of dry wetlands. We found over 580 unique wetlands in the Landsat dataset that were unmapped using the 2008 base imagery. Over 75% of these basins were in the western half of the study area which received approximately 50 cm less rainfall than the eastern half in the year prior to image collection in 2008. To highlight how unpredictable rainfall can be in the region, the western part of the study area received 29 cm of rainfall or 17 cm more than the east in the month following image collection (Oklahoma Mesonet 2015). As a result, had single-date mapping been conducted using imagery from June 2008 rather than May 2008, it would likely have resulted in the identification of more wetlands in the western part of the study area.

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Combining Landsat-derived maps with traditional maps has the potential to improve upon a mapping effort relying on only one of those methods. However, determining accurate wetland boundaries may be a challenge where the two methods differ (Fig. 3). As a result, it is necessary to develop rules to combine datasets that meet the goals of the mapping effort. Since the Landsat mapping is more likely to omit mixed water/upland pixels at the edge of wetlands, manual maps are likely to provide more realistic wetland boundaries in cases where boundaries differ by less than 30 m (the size of one Landsat pixel). In cases where Landsat boundaries are smaller than manual boundaries by greater than 30 m, manual mapping may be overestimating wetland size as a result of extremely wet conditions on the base image. Ultimately, manual quality assurance is likely necessary to delineate final wetland polygon edges. Completing Landsat mapping prior to manual mapping should expedite this process, so polygon boundaries can be determined during mapping and not during map review.

Integrating Landsat wetland maps with manual wetland maps can also serve to improve the hydrological attribution of wetland polygons. Determining wetland hydroperiod from a single base image can be difficult. In fact, several studies have identified the water regime modifier as one of the more problematic attributes of the Cowardin classification to apply (Graves 1991; Cowardin and Golet 1995; Dvorett et al. 2012). However, by observing images from multiple seasons over an extended period, we can not only better estimate the average hydroperiod but also the frequency of years in which the wetland is inundated (Fig. 4). Further hydrological attribution can be added to polygons by incorporating LiDAR data to estimate average and maximum wetland volume and depth.

When calculating volume and depth measurements, researchers must identify those wetlands that likely contained water during LiDAR collection so estimates can be flagged. Furthermore, these calculations should only be conducted for wetlands that exist in topographic depressions and not in other landscape positions such as river terraces. Since the overwhelming majority of wetlands in the region are interdunal depressions and LiDAR was collected during a period when the majority of

wetlands were dry, the hydrologic calculations should provide a reasonably good estimate of volume and depth. Finally, because Landsat pixels are potentially combinations of water and uplands, the estimate of volume for each polygon should be considered approximate. With those caveats in mind, the volume and depth measurements provide useful regional estimates of wetland functions such as water storage and habitat availability. Because the calculations can be applied to any Landsat scene, they can provide a "real-time" regional estimate of the wetland functions provided.

Image Classification

The use of Landsat imagery can improve wetland mapping and hydrologic attribution accuracy, and save time. However, it requires careful consideration of classification techniques, training data, radiometric correction/calibration, and data aggregation from multiple images. We applied several commonly used image classification methods to determine which one worked best for identification of water and interdunal depressions in central Oklahoma. Maximum likelihood (Ozesmi and Bauer 2002), decision tree (Baker et al. 2006), B5 threshold (Frazier and Page 2000), and B5minB3 threshold (Collins et al. 2014) all produced relatively good results for single season classification in the study area. However, we found that B5minB3 produced the best results for the 4 May 2008 image. Several aspects of each classification are worth noting for future wetland mapping efforts. Maximum likelihood had a Kappa statistic similar to other single season classifications but had the lowest Producer's Accuracy for the water class, and many of the omitted pixels were in the center of wetlands. For both Landsat band threshold methods, previously established criteria for class separation created too much confusion between upland and water pixels. Others have found reasonable accuracy by simply applying B5 density slicing on the full spectral range of water pixels (Frazier and Page 2000). However, using density slicing, we found 17% User's Accuracy of the water training pixels alone. Additionally, others have used a B5minB3 < 0 classifier to identify water pixels in playa wetlands of the High Plains of Texas (Collins et al. 2014). This approach led to 44% errors of omission in the water class in our study area. This is likely a result of several characteristics

of interdunal wetlands, including shallow standing water and mixed water/vegetation pixels. While water generally reflects very little in B5, both green vegetation and bare soil reflect substantially more in that band. As a result, when shallow water exists in combination with bare soil or vegetation, it can produce greater values of both B5 and B5minB3. A B5minB3 classifier has the advantage that both soil and vegetation also reflect more than water in B3, somewhat moderating the effect of increased reflectance in B5 (Bowker et al 1985). We found greater classification accuracy when we developed unique decision rules for classification based on manual observation of training pixel spectral histograms. This highlights the point that Landsat classification for wetland mapping will likely need to be regionally developed and validated. Many satellite classifications for wetland mapping (Lunetta and Balogh 1999; Maxa and Bolstad 2009) use one or several images and this may be sufficient in landscapes with less climatic variability between years, such as the northeastern United States. Interdunal wetlands, like other aquatic and wetland systems in the semi-arid Southern Great Plains, can have erratic hydrologic signatures with prolonged dry periods and seasonal variability in inundation (Covich et al. 1997; Johnson et al. 2011). Using multi-season Landsat data helps to identify wetlands with variable inundation patterns but introduces variation into the spectral signature of the land-cover classes used. We found that classifications developed for an early May Landsat image worked poorly with images from the remainder of the year. For example, the water class was confused with evergreen and crop land-cover from the fall through the early spring. Evergreen reflectance increases in the red part of the electromagnetic spectrum (B3) and decreases in near-infrared (B4) under stress, due to reduction in chlorophyll (Mohammed et al. 2000). Drought stress at the end of hot, dry growing seasons in the study area likely made evergreen spectral signatures in the red through near-infrared bands more similar to water, leading to increased misclassification.

The seasonal variability in spectral reflectance of land-cover classes can be accounted for in classification development by including training pixels from multiple images from the same year. By

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incorporating the full range of yearly spectral reflectance for each land-cover class, automated or manual decision criteria to separate classes should be improved. The assumption is that training pixels selected have remained in the same class throughout the period of image inclusion. This can be validated by observing NAIP imagery from the previous and subsequent years. The decision tree developed using the additional training pixels not only reduced upland/water confusion in spring and fall imagery but produced the best results in the accuracy assessment on the 4 May 2008 imagery.

The classification methods that have been developed to identify water in satellite images are plentiful and those applied and evaluated in this paper are not exhaustive. There are several indices available that combine multiple spectral bands into a single value with the intent to optimize separation of water and upland pixels. One such index is the Normalized Difference Water Index (NDWI) calculated as (green – near-infrared) / (green + near-infrared) (McFeeters 1996). Wu et al. (2014) developed a method integrating NDWI with LiDAR-derived depressions to identify vernal pools in Massachusetts, USA with a high degree of accuracy. However, others have found that NDWI creates confusion between water and urban land (Xu 2006). Wu et al. (2014) likely reduced the misclassification of upland sites as wetland by limiting wetland identification to locations in topographic depressions and screening potential vernal pools by land-use.

A second index, the Modified Normalized Difference Water Index (MNDWI) calculated as (green - mid-infrared) / (green + mid-infrared) was developed to assist with reducing the confusion between water and urban pixels found in NDWI (Xu 2006). More recent advancements in water indices show promise in accurately separating water from upland pixels. The Automated Water Extraction Index (AWEI) has been shown to provide greater Landsat water classification accuracy than MNDWI in multiple landscapes (Feyisa et al. 2014). AWEI appears to have a relatively stable threshold value around 0 for separating water from uplands across multiple study regions, but initial assessments have demonstrated that the optimal threshold ranges from -0.15 to 0.045. Additionally, the authors acknowledge that more work is necessary to determine how robust AWEI is to seasonal

variation in water reflectance (Feyisa et al. 2014). Ultimately, supplementing individual Landsat

band reflectance data with multiple water indices (e.g., MNDWI and AWEI) in a decision tree

analysis with multi-season training data may further enhance classification accuracy. We found that

integrating B5-B3 into a decision tree with other spectral bands improved accuracy over a separate

B5-B3 classifier for a multi-season Landsat classification. Decision trees can facilitate optimization

of the classification threshold of indices. Furthermore, including additional bands or indices in the

analysis can potentially provide supplementary data that may reduce the classification confusion to

which each index or band is susceptible.

Map Creation

Finally, for multi-image aggregation, as well as for hydrologic attribution, it is important to

consider criteria for inclusion in the final wetland map. In the semi-arid Great Plains, we need to rely

on long timescales to identify the frequency and duration sufficient to generate wetlands. Therefore,

the general frameworks that have been developed to identify the frequency and duration of saturated

conditions sufficient to generate anaerobic conditions conducive for hydric soil formation may not be

completely appropriate in semi-arid regions. For example, the Natural Resource Council (NRC)

(1995) stated that conditions are sufficient for soil saturation when saturation occurs for 14

consecutive days during the growing season in 50% of years and within the top 30 cm of the soil.

However, these parameters are likely to be too exclusive in the semi-arid plains where long periods of

drought can be followed by deluge periods. As a result, wetlands may be dry for an extended period,

and when inundation occurs, it can last for most of the growing season or over multiple growing

seasons. Tiner (1991) suggests that in semi-arid regions, inundation in 25% of years may be

sufficient to create wetland characteristics. Therefore, all pixels inundated during at least one image

in 25% of the years in this study were included in the final map. Moving forward, multi-image

wetland map generation would be improved by detailed studies of the regional frequency and

duration of inundation necessary to generate wetlands. With this knowledge, regionally appropriate

hydrologic thresholds for inclusion in wetland maps can be refined.

Radiometric Correction

A final consideration in processing satellite imagery for wetland map creation is radiometric

correction. There are a number of both absolute (conversion of satellite measurements to surface

reflectance) and relative (normalization of an image to a reference image) radiometric corrections and

their effectiveness has been evaluated in a number of studies (Song et al. 2001; Paolini et al. 2006;

Schroeder et al. 2006).   We first applied an absolute radiometric correction by converting Landsat

data to top of atmosphere (TOA) reflectance and then used dark object subtraction (DOS) (Chavez

1996). DOS is often used for radiometric correction and is based on the premise that dark objects like

clear, deep water and sloped areas in permanent shadows should have reflectance close to zero in the

absence of atmospheric interference (Chavez 1996). The deviation of these dark objects from

zero/low reflectance can then be attributed to atmospheric effects and the remainder of the scene can

be corrected to the minimum value of each band. Song et al. (2001) found that DOS produced

consistent results for both classification and change detection studies. However, when valid dark

objects are absent from an image, DOS can produce spurious results (Chavez 1996) because deviation

from zero/low reflectance potentially results from the true spectral characteristics of the object. This

appeared to be the case for our study area, which lacks typical dark objects like sloped areas in

permanent shadow due to relatively flat topography, and clear water due to regionally high turbidity.

When DOS failed to provide sufficient correction, we used LEDAPS surface reflectance

datasets processed with the MODIS/6S absolute atmospheric correction algorithm (Vermote et al.

1997; Masek et al. 2013). In addition to atmospheric correction, the LEDAPS algorithm addresses

the other sources impacting radiometric responses (Masek et al. 2013), including differences between

sensors (LT5 and LE7), changes in sensor calibration over time, and illumination and observation

angles (Paolini 2006). In 2003, the LEDAPS calibration was updated to correct for degradation of sensors and the internal calibrator using an exponential decay model based on a simultaneous collection of LT5 and LE7 scenes (Teillet et al. 2004; Masek et al. 2013).

Others have found that using radiometric normalization after applying LEDAPS algorithms improved image correction (Huang et al. 2014). Schroeder et al. (2006) found that correcting one reference image using the MODIS/6S correction (Vermote et al. 1997) and normalizing other Landsat scenes using multivariate alteration detection (MAD) (Canty et al. 2004) produced better results than absolute correction of all images using MODIS/6S. However, the MODIS/6S correction used did not appear to also include the exponential decay models of the LEDAPS algorithm to account for LT5 sensor degradation (Schroeder et al. 2006). This may partially account for the reduced accuracy. We found that applying radiometric normalization using IR-MAD after LEDAPS correction did little to alter the classification results. Normalizing the 2 May 2010 image to the 4 May 2008 IR-MAD changed the class of less than 0.03% of the pixels. Furthermore, the pixels removed from the water class were equally likely to be water as those added to the water class. This does not indicate that radiometric normalization fails to reduce inconsistencies in spectral reflectance in multi-temporal data due to a potentially incomplete absolute correction. Rather, for this study LEDAPS correction was sufficient to address the potential sources of error in spectral reflectance, allowing us to accurately apply the binary water/upland classification on multiple Landsat scenes. Additional work to evaluate the accuracy of LEDAPS surface reflectance data would help to determine the sufficiency of the correction used for future Landsat-based wetland mapping applications. It is also worth noting that in projects that use multi-season imagery, problems may arise when normalizing to a reference image from another season, where spectral differences between scenes are too great (Canty and Nielsen 2008).

*Conclusion*s

Accurate wetland maps are fundamental for effective monitoring and management of wetland resources. Advances in remote sensing since NWI protocols were initially developed in the 1980s provide an opportunity to improve map accuracy, where high resolution single date imagery fails to consistently identify the spectral signature of regional wetland classes. Combining Landsat classification with manual mapping is a method that takes advantage of high recurrence imagery, while minimizing the shortcomings of the 30 m spatial resolution of Landsat. The development of a protocol to identify wetlands using high-recurrence satellite imagery must address several non-trivial facets, including training data, radiometric correction, classification technique, and aggregation of multiple classified images into a final wetland map. Likely, many of these facets will be specific to the project of interest, resulting from regional characteristics. For example, regional wetland classes and classification confusion with other land-covers will dictate which classification methods are appropriate. Seasonal and inter-annual patterns of inundation will inform the decision of images selected for inclusion. However, we hope that by providing an example of a multi-year, multi-season, Landsat-based wetland mapping effort, and outlining important aspects of classification for consideration, future efforts will be benefited.
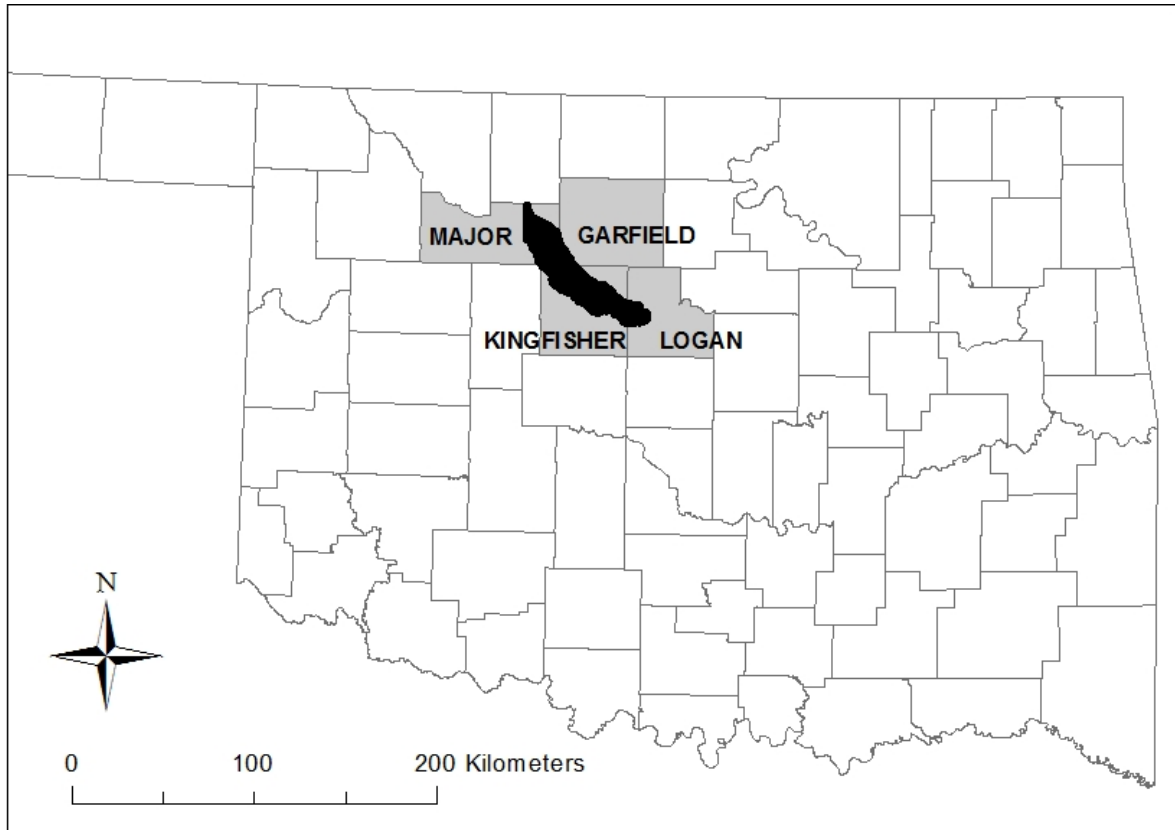
Figure 1. The portion of the Cimarron River Pleistocene Sand Dunes Ecoregion in Oklahoma for which mapping was completed is highlighted in black and includes portions of four counties (Garfield, Kingfisher, Logan and Major) highlighted in gray.
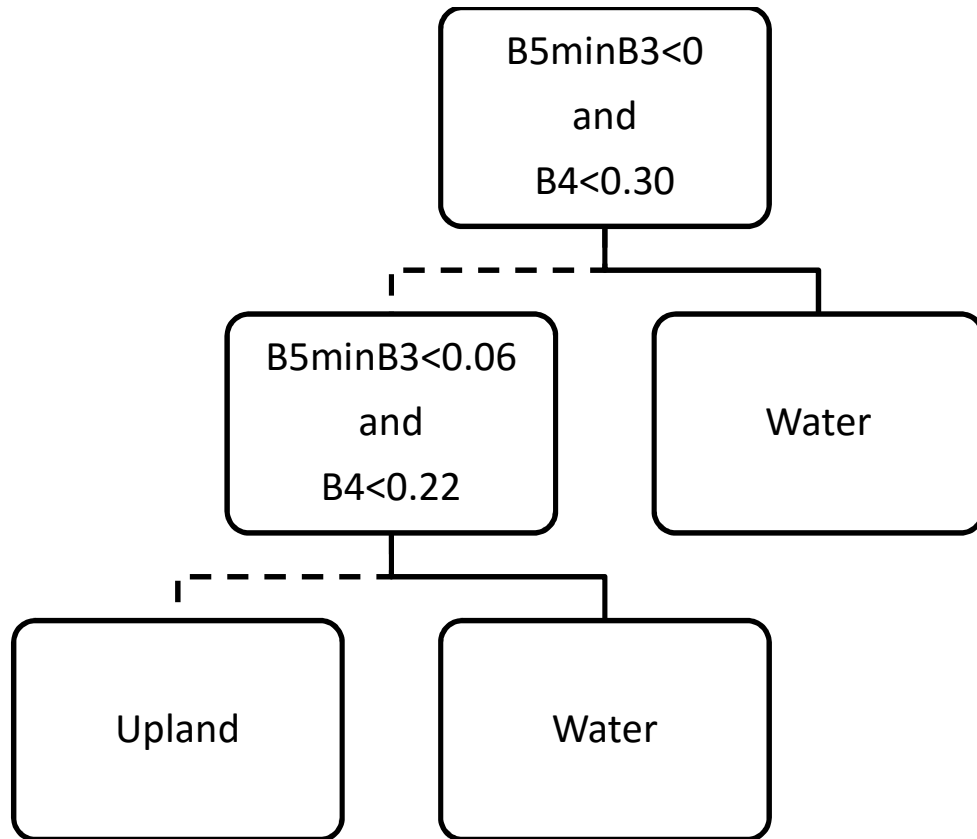
Figure 2. Final decision tree to classify Landsat imagery for water identification in the Pleistocene Sand Dunes Ecoregion of the Cimarron River in central Oklahoma. B5MINB3 is Band 5 minus Band 3 and B4 is Band 4. Solid lines denote that the criteria of the previous node are true and dashed lines are false.
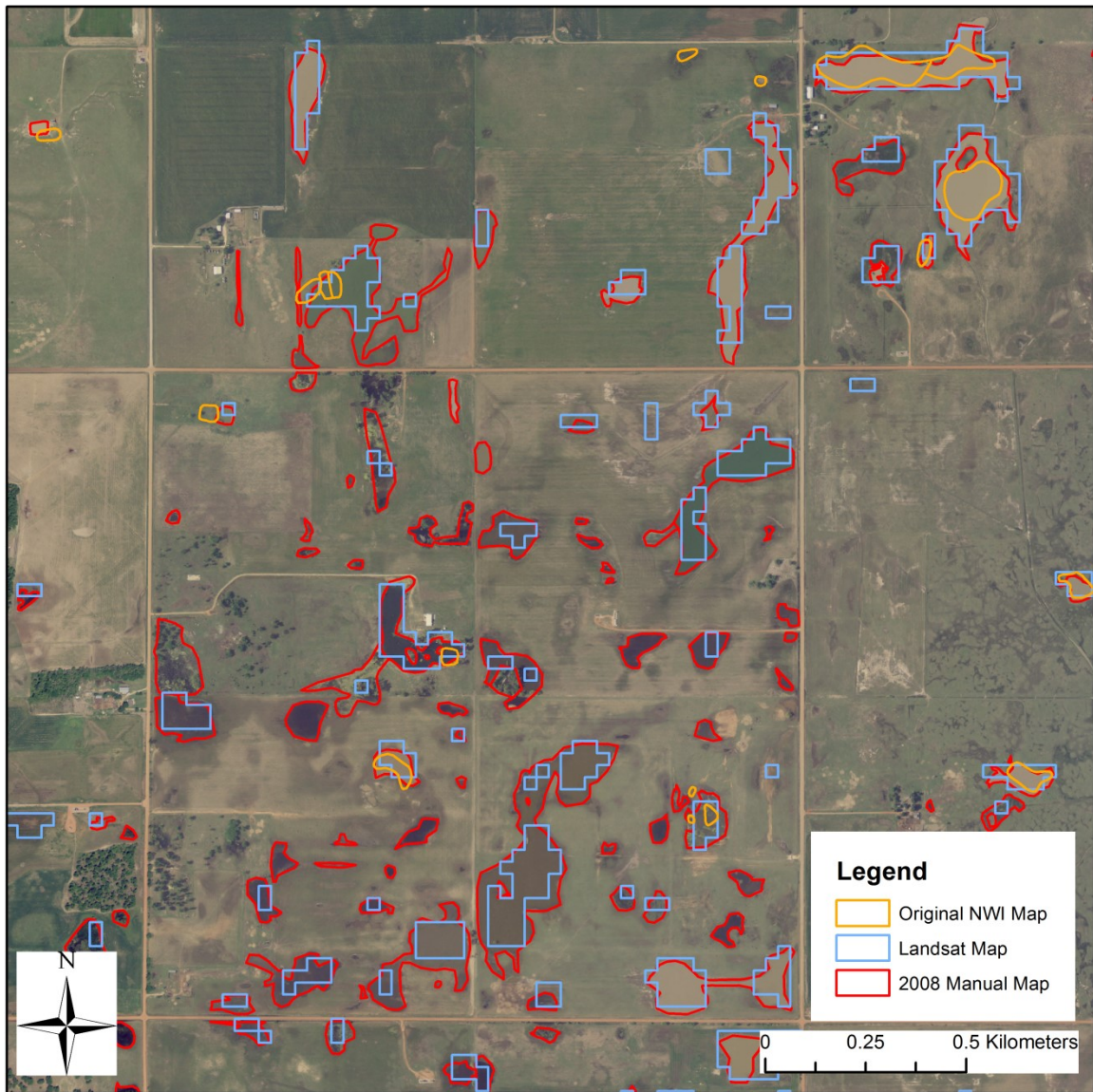
Figure 3. 2008 National Agricultural Imagery Program image overlain with the original NWI map (orange), Landsat-derived map (blue), and the manual map digitized from 2008 imagery (red) for a portion of Kingfisher County in the Pleistocene Sand Dune Ecoregion of central Oklahoma.
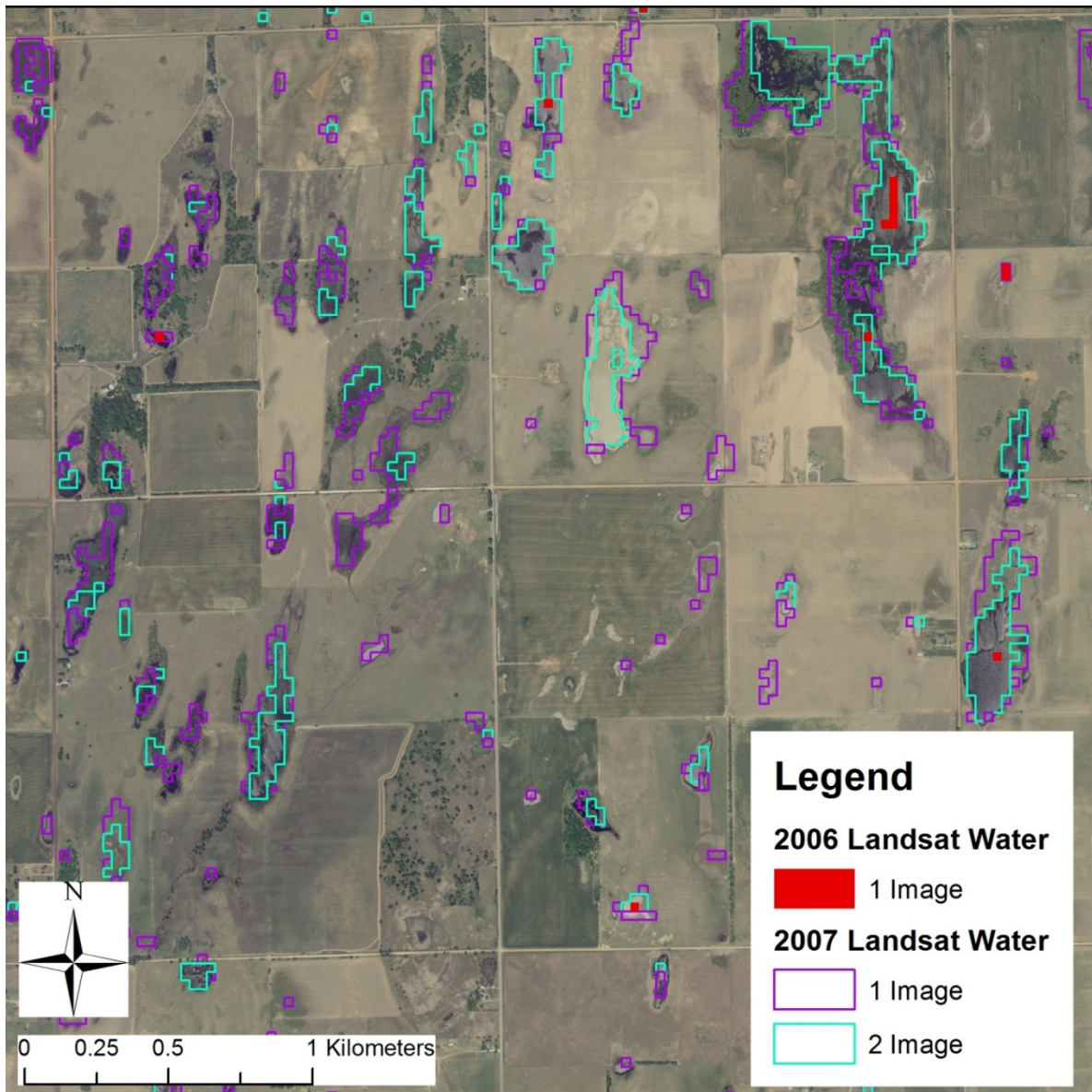
Figure 4. Portion of Garfield County in the study area in Oklahoma highlighting water variability in interdunal depressional wetlands. Purple boundaries represent areas inundated for one of three Landsat images in 2007 and light blue boundaries were wet for two consecutive Landsat images. Solid red polygons denote areas that were wet for one Landsat images in 2006. In 2006, no wetlands held water for two consecutive images in this part of the study area. Polygons are overlaid on 2008 National Agricultural Imagery Program aerial imagery.

Table 1. List of Landsat images from Path 28 Row 35 in the Pleistocene Sand Dunes Ecoregion of central Oklahoma classified using decision tree analysis to identify water pixels. Images were aggregated to determine the inundation frequency of individual pixels and to ultimately develop wetland maps.

Date	Landsat	Date	Landsat
4 December 1993	LT5	21 January 2003	LT5
30 June 1994	LT5	9 July 2003	LT5
5 November 1994	LT5	13 October 2003	LT5
9 January 1995	LT5	19 February 2004	LT5
20 August 1995	LT5	12 July 2004	LT5
23 October 1995	LT5	16 October 2004	LT5
16 March 1996	LT5	20 January 2005	LT5
6 July 1996	LT5	28 June 2005	LT5
10 October 1996	LT5	3 November 2005	LT5
2 March 1997	LT5	23 January 2006	LT5
24 July 1997	LT5	1 July 2006	LT5
12 October 1997	LT5	21 October 2006	LT5
22 March 1998	LT5	27 February 2007	LT5
29 August 1998	LT5	5 August 2007	LT5
11 May 1999	LT5	1 March 2008	LT5
22 July 1999	LE7	23 July 2008	LT5
10 October 1999	LE7	27 October 2008	LT5
8 February 2000	LT5	16 February 2009	LT5
26 August 2000	LE7	20 April 2009	LT5
14 November 2000	LE7	29 October 2009	LT5
2 February 2001	LE7	12 July 2010	LT5
17 June 2001	LT5	3 December 2010	LT5
15 October 2001	LE7	5 January 2011	LT5
13 February 2002	LT5	29 June 2011	LT5
16 September 2002	LE7	19 October 2011	LT5
19 November 2002	LE7		

Table 2. Summary of the accuracy of classification methods applied to Landsat scenes from Path 28 Row 35. B5 is band 5 threshold. B5minB3 is Band 5 minus Band 3 threshold. ML is maximum likelihood, and DT is decision tree. These methods use single-date training data. We also used DT with training data from four seasons. All classifications were applied to the Landsat scene from 4 May 2008, except for the last which was applied to 2 May 2010 imagery.

Method	Landsat class	Validated Class		User's Accuracy
		water	upland	
B5<0.13	water pixels	168	32	84.00
(4 May 2008)	upland pixels	12	988	98.80
	Producer's Accuracy	93.33	96.86	
	kappa= 0.86			
B5minB3<0.065	water pixels	188	12	94.00
(4 May 2008)	upland pixels	11	989	98.90
	Producer's Accuracy	94.47	98.80	
	kappa= 0.93			
DT	water pixels	166	34	83.00
B4<0.21 and	upland pixels	17	983	98.30
B5minB3<0.16	Producer's Accuracy	90.71	96.66	
(4 May 2008)	**kappa= 0.84**			
ML	water pixels	185	15	92.50
(4 May 2008)	upland pixels	36	964	96.40
	Producer's Accuracy	83.71	98.47	
	kappa= 0.85			
DT with all	water pixels	197	3	98.50
season training	upland pixels	12	988	98.80
data	Producer's Accuracy	94.26	99.70	
(4 May 2008)	**kappa=0.96**			
DT with all	water pixels	187	13	93.50
season training	upland pixels	1	199	99.50
data	Producer's Accuracy	99.47	93.87	
(2 May 2010)	**kappa=0.93**			

Table 3. (a) Agreement of Landsat-derived wetland map with the updated NWI map and the original NWI map by size class. Unique columns denote the number of polygons in the Landsat-derived map not mapped in the updated NWI or the original NWI, respectively. (b) Agreement of updated NWI map with the Landsat-derived wetland map and the original NWI map by size class. Unique columns denote the number of polygons in the updated NWI map not mapped in the Landsat-derived map and the original NWI, respectively.

(a)
Landsat-derived Wetlands

Size (ha)	Polygons	% Updated NWI Agreement	Unique	% Original NWI Agreement	Unique
0.0-0.18	1675	77.1	383	27.7	1211
0.18-0.54	797	81.6	147	34	526
0.54-1.98	512	90.2	50	44.1	286
>1.98	172	95.3	8	63.4	63
Total	3156	81.3	588	33.9	2086

(b)
Updated Manual NWI

Size (ha)	Polygons	% Landsat Agreement	Unique	% Original NWI Agreement	Unique
0.0-0.18	3151	10.4	2823	17.2	2609
0.18-0.54	1568	45.3	857	29.1	1112
0.54-1.98	971	67.6	315	33.2	649
>1.98	383	84.6	59	55.1	172
Total	6073	33.2	4054	25.2	4542

Table 4. Results of "windshield" field verification of 30 wetland polygons mapped using 2008 base imagery manual map only (manual), 30 from Landsat-derived map only (digital), and 30 mapped using both methods (agree). Sites counted as wetland had either hydrological indicators or hydrophytic vegetation or both. Sites listed as upland lacked hydrological indicators and hydrophytic vegetation, did not occur in a basin, and were surrounded by unfarmed land-use. Sites were removed from the accuracy assessment if they could not be seen from the road, if they had been lost to development, or if the wetland-status was undeterminable. Undeterminable wetlands lacked wetland indicators (hydrology or hydrophytic vegetation), occurred in a topographic basin, and were farmed. Accuracy measurements were calculated by dividing the number of confirmed wetland sites by the sum of the confirmed wetland sites and the uplands included in the map.

Map Type	Wetland	Upland	Removed (no visibility)	Removed (lost)	Undeterminable	Accuracy
Manual	22	2	0	1	5	91.67
Digital	14	2	2	2	10	87.50
Agree	23	0	2	0	5	100.00

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CHAPTER II

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PREDICTING INUNDATION AND VULNERABILITY OF DEPRESSIONAL WETLANDS

TO CLIMATE CHANGE WITH REMOTELY SENSED DATA

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Abstract: Climate projections of more extreme storm events and more severe droughts in the Great Plains of North America indicate that the hydrological functions of surface water fed depressional wetlands are likely to change. Regional hydrological models are necessary to determine how wetlands will respond to different climate change scenarios. We developed a model to predict wetland inundation using freely available data that included climate (precipitation), local (wetland size) and landscape variables (watershed land-use) in the Pleistocene Sand Dunes Ecoregion of central Oklahoma. Rainfall quantity, timing and intensity were all important in predicting wetland inundation. Additionally, more rainfall was required to inundate wetlands during long-term droughts, indicating that climatic conditions that occurred in previous seasons and years are also critical in affecting wetland hydrology.   Furthermore, small wetlands in grassland watersheds required more rainfall than larger agricultural wetlands. As a result, we predict that small wetlands surrounded by grasslands are more likely to experience reduced inundation frequency under increased drought conditions predicted for the future. Since wetland dependent taxa rely on the hydrological cycles within wetlands and connectivity between available habitats, it is critical to understand how future climate scenarios may impact wetland inundation at both local and regional scales. Management of the structure and density of aboveground cover in grasslands with fire and grazing may be necessary to increase runoff to wetlands and maintain current inundation frequency and connectivity in the future.

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1 INTRODUCTION

Depressional wetlands provide critically important ecosystem functions such as nutrient cycling, aquifer recharge and habitat provisioning. The degree to which these functions are provided is largely driven by the frequency, timing, duration and extent of inundation events. For example, the ability of wetlands to effectively transform nutrients depends on shifts from anaerobic to aerobic conditions both spatially and temporally (Mitsch and Gosselink 2007). Future climate projections indicate considerable changes to precipitation quantity and intensity, as well as increased evaporative potential from greater temperatures (Shafer et al. 2014; Christensen et al. 2007). Consequently, it is likely that not only patterns of wetland inundation (e.g., frequency, timing, and length of flooding) will be significantly affected, but the functions that these ecosystems provide will likely be impacted as well (Meyer et al. 1999; Burkett and Kusler 2000). In fact, numerous studies at multiple scales forecast potential climate change impacts to wetland hydrology (Acreman 2009), as well as alterations to wetland distribution (Garris et al. 2015), wetland size, vegetation structure (Poiani and Johnson 1993; Johnson et al. 2005), habitat quality for waterfowl (Sorenson et al. 1998), water storage capacity and nutrient cycling (Pitchford et al. 2012).

Wetlands in the Southern Great Plains of North America are at great risk to alterations from climate change where evapotranspiration greatly exceeds precipitation under current conditions (Oklahoma Mesonet 2015). As a result, many topographic

depressions already exist at the fringe of hydrologic sufficiency necessary to maintain the anaerobic soil conditions that promote biogeochemical and habitat functions (Dvorett et al. 2016). In the Great Plains, average annual temperature is projected to increase by 2.6 to 5.4 C for the period from 2080-2099 (Christensen et al. 2007) which will likely result in even greater evaporative losses from surface water bodies (Meyer et al. 1999). While there is greater uncertainty in the projections for future precipitation quantity (Christensen et al. 2007; Zhang et al. 2011; Sunyer et al. 2012), climate models have predicted a greater percentage of precipitation falling in fewer events with longer periods occurring between precipitation events (Karl et al. 2009; Shafer et al. 2014). Regional climate models for the Central Great Plains (e.g., Oklahoma), project increases to total spring rainfall and the size of the most intense spring rainfall events (Qiao et al. Unpublished). Predicted increases of 1 to 1.5 cm for the highest intensity spring events (Qiao et al. Unpublished) are likely to increase infiltration excess runoff, the dominant runoff mechanism to low-lying depressions in semi-arid regions (Pilgrim et al. 1988). However, models also project a decrease in the quantity of summer rainfall leading to more frequent and severe droughts (Christensen et al. 2007; Qiao et al. Unpublished), and subsequently, decreased soil moisture levels. While antecedent soil moisture is unlikely to have a large impact on runoff generated during the highest intensity storm events, it has been shown to be an important determinant of runoff from small to moderate storms (Castillo et al. 2003). The low antecedent soil moisture in uplands during drought will likely reduce the runoff to low-lying depressions during small to moderate storm events, potentially offsetting the increased runoff during the predicted higher intensity storms.

Ultimately, due to the numerous factors driving rainfall-runoff relationships such as soil infiltration capacity, slope, and plant interception, regionally specific hydrologic models are necessary to accurately predict potential impacts to wetlands from climate change. Furthermore, given the functional importance of depressional wetlands, it is critical that planning tools exist to help understand and mitigate climate change induced hydrologic alterations. Regional probabilistic hydrologic models are one such planning tool and can provide insight into the climatic drivers of wetland hydrology. When combined with climate projections, regional hydrologic models can elucidate broad scale changes to wetland hydrology within the area of interest (Acreman et al. 2009). For example, regional models have been applied successfully to other regions such as the Prairie Pothole Region to predict the number of inundated depressional wetlands based on precipitation and drought severity using linear regression (Larson 1995; Sorenson et al. 1998). By understanding the relationship between drought severity and wetland inundation, Sorenson et al. (1998) were able to make predictions of the percentage of regionally inundated wetlands under scenarios of increased temperature as well as increased and decreased precipitation.

A disadvantage of regional models is that they do not identify the wetlands most at risk to hydrological alteration from climate change. Understanding the attributes of wetlands that may make them more vulnerable to reduced inundation can be critical for the development of restoration and conservation priorities. Deterministic models, which include all processes relevant to wetland hydrology, are extremely useful for predicting with great accuracy the hydrologic attributes of specific wetlands (Poiani et al. 1996). Furthermore, deterministic models have been developed successfully for depressional

wetlands in several regions (Mansell et al. 2000; Su et al. 2000; Boone et al. 2006; Sun et al. 2006). However, deterministic models generally require a large amount of site-specific information such as groundwater inflow and soil hydraulic gradient, which requires considerable time and effort to develop the model and limits model inference to a small subset of wetlands (Acreman et al. 2009). In this study, we developed a regional probabilistic hydrologic model for predicting inundation events in small depressional wetlands, but predict inundation at the individual wetland level. As a result, the model can generate predictions for regional hydrologic change as well as identify site specific characteristics (e.g., wetland size and surrounding land-use) that may make certain wetlands more susceptible to climate change impacts. Furthermore, because the data inputs are all from freely available remotely sensed data sources, this approach can be rapidly implemented with minimal cost.

2 METHODS

2.1 Study area

The study area includes the eastern half of the Pleistocene Sand Dunes Ecoregion (Omernik 1987) adjacent to the Cimarron River in central Oklahoma and encompasses portions of four counties (Garfield, Kingfisher, Logan and Major) within an approximately 1300 sq. km area (Figure 1). Climate is semi-arid with evapotranspiration greatly exceeding precipitation. Average yearly rainfall is approximately 83 cm in the eastern part of the study area and decreases to 75 cm in the west. Rainfall is highly variable between years, with yearly rainfall ranging from 53 cm (2012) to 145 cm (2007) during the last 10 years (Oklahoma Mesonet 2015). On the leeward terraces of the Cimarron River, aeolian dune formation and migration have occurred during episodic

droughts, the last of which occurred approximately 800-900 years ago. In the valleys of the now stabilized dune fields, the area has abundant temporary interdunal depressional wetlands (Lepper and Scott 2005). The study area is perhaps the largest aggregation of wetlands in central Oklahoma, with an average density of 4 wetlands per sq. km (Dvorett et al. 2016*).* The majority of wetlands in the study area are small with more than 80% < 0.5 hectares and approximately 6% are larger than 2 hectares. Inundation of these systems is primarily dependent on the precipitation that occurs in small watersheds. The predominant land-use in the study area is agricultural, with the primary crops being rye (*Secale cereale*) and wheat *(Triticum aestivum*).

2.2 Wetland inundation

Wetland inundation was determined using 57 classified Landsat 5 and Landsat 7 images from a single scene (Path 28 Row 35) from the winter of 1995 to the winter of 2011 (USGS 2015). Images were classified into water and upland pixels using a decision tree analysis on Landsat spectral bands 3, 4 and 5 specifically designed for the region and resulting in a high accuracy (kappa>0.93). The kappa statistic is a measure of observed accuracy of a classification compared to the expected accuracy. Values of kappa range from 0 to 1 with values above 0.8 considered an excellent classification (Landis and Koch 1977).   Dvorett et al. (2016*),* outline detailed methods on the Landsat classification methods used. We applied the change detection tool in ENVI 5.2 (Exelis Visual Information Solutions, Boulder, Colorado) to identify wetlands that became inundated and those that remained dry between subsequent Landsat scenes. A wetland was deemed inundated when it was completely dry in the first image of a pair and contained at least one pixel (0.09 ha) of water in the second image. A wetland was deemed dry if it did not

contain water in either the first or second scene. Finally, all wetlands that began the

period inundated were removed from the analysis because the focus of this study was on

the climatic conditions necessary to cause inundation. While each Landsat scene is

collected every 16 days, paired images for the change detection were 48 to 96 days apart

because of the availability of Landsat scenes with <10% cloud cover and no popcorn

clouds (isolated cumulus or stratocumulus clouds) (Collins et al. 2014).

2.3 Datasets

This study included 497 wetlands that ranged in size from 0.36 ha to 22.23 ha and

had no indication of hydrological alteration due to excavating or ditching. Inundation at

these wetlands was identified from the paired classified Landsat images described above.

Explanatory variables used to predict wetland inundation included (1) total rainfall for the

96 days prior to the second Landsat image, (2) maximum 24 hour rainfall event for the 96

days prior to the second Landsat image, (3) Palmer Drought Severity Index (PDSI;

Palmer 1965) 96 days prior to the second Landsat image, (4) watershed size, (5) wetland

size, (6) season, (7) percent agriculture in the watershed and (8) average soil drainage

class in the watershed. We calculated total and maximum rainfall from the National

Weather Service (NWS) Arkansas-Red Basin River Forecast Center daily precipitation

dataset. The NWS precipitation data is a 16 sq. km grid that combines rain gauge data

with radar based interpolation methods (NWS 2015). Historical PDSI data was

downloaded from the National Oceanographic and Atmospheric Administration (NOAA)

National Center for Environmental Information (NOAA 2015). We delineated

watersheds for each wetland using the depression evaluation tool in ARC MAP 10.1

(ESRI, Redlands, California) and 1 m spatial resolution Light Detection and Ranging

(LiDAR) elevation dataset. LiDAR data were generated by the USDA Natural Resources Conservation Service (NRCS) in January 2012 with 18.5 cm vertical accuracy and 1.4 m point spacing (NRCS 2012). Wetland size was derived from wetland maps created by Dvorett et al. (2016). Seasons were grouped using meteorological divisions as follows, March through May (spring), June through August (summer), September through November (fall), and December through February (winter) We calculated percentage agricultural land-use in each watershed delineated for study wetlands using the 2011 National Land Cover Dataset (Homer et al. 2011). For each wetland, a soil drainage class was calculated as a weighted average in the surrounding watershed from the NRCS Soil Survey Geographic Database (SSURGO) (SSURGO 2015). Drainage classes A through D were converted to 1 through 4, with 4 generally having the lowest hydrologic conductivity and highest water table (Soil Survey Division Staff 1993).

2.4 Hydrologic Model

Wetland inundation was predicted using a model selection approach (Burnham and Anderson 2002) for logistic regression using the package MuMIn (Barton 2016) in program R (R Core team 2013). We considered models with all combinations of explanatory variables, as well as interaction effects between season and total rainfall, as well as season and maximum rainfall. Models with Delta Akaike Information Criteria (ΔAICc) <4 were considered candidate models (Akaike 1974). For the selected model, we calculated odds ratios and marginal effects. Marginal effects represent the change in inundation probability when a variable is increased one unit and all other variables are held constant at their mean (Long and Freese 2003). We assessed multicollinearity with variance inflation factors (VIFs) using the package rms (Harrell, Jr. 2015) in program R.

Inundation data from 1995 to 2006 were used for model calibration and the remainder of the dataset from 2007 to 2011 was used for model validation. We assessed model fit with McFadden's R^2, a measure of the improvement of the candidate model over the null model (McFadden 1974) and area under the curve (AUC) for the receiver operating characteristic (ROC). AUC is a measure of probability that a true positive value (indicating an inundated wetland) will have a greater model predicted probability of inundation than a true negative value (indicating a dried wetland) (Hanley and McNeil 1982). A predicted probability cutoff for spring inundation was calculated by maximizing the kappa statistic for the validation dataset using package SDMtools (VanDerWal 2015) in Program R. All probabilities above the probability cutoff were then predicted to be inundated for model validation. The probability cutoff was maximized for only spring inundation events because of the preponderance of spring inundation (45% of all inundation events in the study period). Additionally, the best candidate models identified in the model selection had higher inundation probabilities at lower values of total summer rainfall and maximum winter rainfall. Poor prediction accuracy would likely result from using negative rainfall model coefficients in the summer and winter.

2.4 Projections for wetland inundation

Using the hydrologic model, we predicted potential changes to spring wetland inundation. We adjusted the precipitation and PDSI values for the full model run from 1995 to 2011 to account for different future climate scenarios and to represent a potential future 15 year period at the end of the century. Climate projections for the Central Great Plains of Oklahoma predict an increase in total spring rain (Christensen et al. 2007), an

increase in spring rain intensity and increased periods of prolonged drought by the end of the century (Karl et al. 2009; Shafer et al. 2014; Qiao et al. Unpublished). Scenarios included (1) increasing total rain by 10% and max rain by 1.5 cm (+MAX), (2) increasing only total rain (+TOT), (3) increasing total rain, max rain, and drought by -2 PDSI (+MAX-PDSI), (4) increasing total rain and drought (+TOT-PDSI), and (5) increasing only drought (-PDSI). We then compared the predicted frequency of inundation during the period from 1996 to 2011 with the predicted frequency of inundation for each 15 year future scenario.

3 RESULTS

3.1 Hydrologic model

VIFs indicated no signs of multicollinearity (values < 3) (Zurr et al. 2010); therefore, all variables were included in the model selection. We found four possible candidate models with ΔAIC < 4 (Table 1). Although the global model was the top candidate model, we chose the model with all variables except soil drainage and watershed size, which had a ΔAIC = 2.59. When watershed size and soil drainage were removed from the model, McFadden's R^2 only dropped 0.0005 from 0.3316 in the global model to 0.3311 in the reduced model, indicating the variables explained an extremely small amount of the variation in the dataset. These variables were most likely included in the top model because of the large sample size and resultant high statistical power, despite their inability to explain much variation in the dataset. AUC statistics for the calibration dataset (AUC=0.86) and the validation dataset (AUC=0.81) indicated that the model fits the data and predicts future inundation events well (Hanley and McNeil 1982).

The model coefficients, odds ratios and marginal effects for the selected model are presented in Table 2. We found that smaller wetlands and wetlands within grassed catchments are less likely to be inundated than larger wetlands in agricultural catchments. For every hectare increase in wetland size, inundation probability increases by approximately 3.5% when holding all other variables at their mean. Furthermore, wetlands in agricultural watersheds are approximately 7% more likely to be inundated than wetlands surrounded by grassland. Additionally, as drought increases (lower values of PDSI), more rain is required to inundate wetlands due to the drier conditions. For example, a 1 unit increase in drought severity on the PDSI in the spring is approximately equal to the loss of one cm of total rain.

Not surprisingly, the amount of rainfall is a good predictor of wetland inundation, but timing and intensity of rainfall are also important factors in predicting inundation. In the spring, both total and maximum rainfall are good predictors of inundation (marginal effects of 0.034 and 0.05, respectively). In the summer, maximum rainfall becomes more important in predicting wetland inundation (marginal effect of 0.09), while the model predicts that increases in total precipitation actually make wetlands less likely to become inundated. In reality, the negative relationship is more likely a time of season effect. The earliest five summer time periods (Landsat pairs occurring in June) accounted for the majority of summer inundation events despite averaging approximately 10 cm less rainfall than the latest five summer time periods (Landsat pairs occurring from the end of July through end of August). This is likely a result of wetlands being subjected to significantly higher rates of evapotranspiration and decreased soil moisture by the end of the summer.

In the winter, the effect of total rainfall is similar to the spring (marginal effects of 0.03 and 0.034, respectively) but maximum rainfall negatively predicts inundation. This is likely due to a low occurrence of large precipitation events in the winter; only 10% of the wetlands in the winter experienced greater than 5 cm maximum rainfall and 2% received greater than 6 cm rainfall. By comparison, during the remainder of the year, 38% of wetlands received greater than 5 cm rainfall and 23% received greater than 6 cm rainfall. In the fall, inundation probability increased with increases in maximum and total rainfall. Maximum rainfall was a better predictor, but both variables had lower marginal effects in the fall when compared to the spring, indicating a weaker influence of rain on probability of inundation.

3.2 Climate projections

Using the validation dataset, we identified a probability cutoff for model output to maximize the kappa statistic for correct classification of wetland inundation. The optimal probability cutoff point was 0.62 with a kappa of 0.42. For the entire dataset, the model predicted spring inundation with 83% accuracy. Table 3 displays the predicted percentage of wetlands that would be inundated under normal and drought conditions while varying maximum and total rain. Shifting from normal drought conditions (0 PDSI) to extreme drought conditions (-5 PDSI) requires approximately 5 centimeters more of total rain to inundate all study wetlands. Furthermore, increasing storm intensity by 2 cm reduces the total rain necessary to inundate all the study wetlands by approximately 3 cm. This highlights the interaction between high intensity storms, seasonal rainfall and long-term drought conditions in causing wetland inundation.

Additionally, we predicted spring inundation under 5 different future climate scenarios for the end of the 21st century, and determined for each wetland the percentage change in the frequency of spring inundation events. Scenarios +MAX and +TOT predict that 49% and 25% of wetlands will increase in spring inundation frequency, respectively, while the remainder will be unchanged (Figure 2). When drought is increased for scenarios +MAX-PDSI and +TOT-PDSI, the number of unchanged wetlands increase to 72% and 95%, respectively. Finally, under a scenario with increased drought but no increase in precipitation, 41% of the wetlands are predicted to decrease in frequency of inundation with the remainder unchanged.

Because the model indicates that small wetlands in grassed catchments require more rainfall to inundate than large wetlands surrounded by crops, changes in climate patterns may impact these wetlands differently. With a 4.6 cm maximum rainfall (average for period of observation) and a PDSI of 0, a 3 ha wetland surrounded by agriculture is predicted to become inundated with total rainfall of 16.4 cm, or less than the 96 day total rainfall mean for the period (16.7 cm; Figure 3). Under the same conditions, a 0.4 ha grassland wetland is predicted to become inundated with 21.3 cm of total rainfall. To inundate the same small grassed wetland under moderate (PDSI -2.5), severe (PDSI -3.5) and extreme (-4.5 PDSI) drought conditions would require increases of total rain to 21.6 cm, 22.6 cm and 23.6 cm, respectively, even with 6.1 cm maximum rainfall (a 1.5 cm increase). These are increases of 29%, 35% and 41%, respectively, to the 96 day total rainfall average for the period of observation. On the other hand, for the same maximum rainfall event, a large agricultural wetland under moderate drought conditions is predicted to become inundated with the average total rainfall for the study

period. Severe and extreme drought would only require increases of 6% and 12%, respectively, above current average total rainfall.

4 DISCUSSION

There is a need for regional-based hydrologic models to assess the impacts of climate change on wetlands (Acreman et al 2009). One main advantage of these models is that they provide guidance for setting restoration and conservation priorities at a scale suitable for management (e.g. within the jurisdiction of a state or within a watershed planning unit). The approach we used to model wetland inundation in this study has several additional advantages. Firstly, we relied entirely on freely-available, easily-acquired remotely-sensed datasets. This makes it possible to develop models relatively rapidly and cost-effectively. Secondly, by modeling inundation of a large number of individual wetlands, we cannot only model region-wide changes to hydrology resulting from future climate scenarios, but we can begin to predict which wetlands in the region might be more vulnerable to climate change based on their size and surrounding land-use.

Our model predicts that smaller wetlands in grassland catchments are less likely to become inundated than larger wetlands surrounded by agriculture. This indicates that not all wetlands in the region are likely to be impacted similarly by climate change. For example, small grassed wetlands will require dramatic increases in average spring rainfall to become inundated during the increased drought conditions predicted for the future (Fig 3). The relationship between wetland size and inundation likely results from larger wetlands having larger watersheds and therefore, a greater runoff potential. Larger playa wetlands in the Southern High Plains of Texas (Johnson et al. 2011) and the Rainwater Basin Region of Nebraska (Cariveau et al. 2011) had a higher inundation probability than

smaller wetlands. It is also possible that the effect is overestimated in our study due to the relatively long interval between Landsat images (up to 96 days). Smaller wetlands tend to have shorter hydroperiods (Snodgrass et al. 2000). Therefore, it is possible that a small wetland with a short average inundation length (e.g., 31 days) could be filled by a storm event and dry in the 96 day interval between Landsat images included in the study.

We also found that wetlands surrounded by agriculture were more likely to become inundated than wetlands surrounded by grassland. Studies assessing the inundation probability of playa wetlands also found strong land-use influences on wetland hydrology (Cariveau et al. 2011; Johnson et al. 2011). In Nebraska, wetlands surrounded by native rangeland were more likely to become inundated than wetlands with agricultural watersheds, while wetlands surrounded by Conservation Reserve Program (CRP) grasslands were less likely to be inundated than wetlands with agricultural watersheds (Cariveau et al. 2011). Dense non-native grass buffer strips, similar to the vegetation of some CRP plantings, have been shown to reduce the amount of runoff to low-lying depressional wetlands (Van Dijk et al. 1996; van der Kamp et al. 2003). Managing the density and structure of vegetation in grasslands appears to be a critical factor in determining wetland inundation frequency. In fact, fire and grazing management practices have been shown to increase inundation rates (Pyke 2005; Voldseth et al. 2007; Voldseth et al. 2009). Due to landowner privacy issues associated with CRP, we were unable to determine which wetlands were surrounded by CRP grasslands. However, during the course of research in the region, we determined that many of the wetlands are indeed surrounded by the dense stands of non-native grasses common to CRP plantings. It is possible that CRP plantings in our study region may be

explaining the relationship between inundation and land-use. Furthermore, eastern red cedar (*Juniperus virginiana*) encroachment, which has expanded due to fire suppression and poor land management in the region (Fuhlendorf et al. 2008), may also play a role in reduced wetland inundation in grasslands. Conversion of grassland to stands of cedar has been shown to reduce surface runoff due to increases in saturated infiltration capacity and decreases in soil moisture (Zou et al. 2014). As of 1994, over 160,000 hectares of rangeland in our study counties (over 15% of the total area) were invaded with eastern red cedar (Bidwell et al. 1994), and cedar expansion has continued in the last 20 years.

Additionally, although agricultural wetlands were more easily inundated in our study area, it is possible that these wetlands exhibit degradation to other aspects of hydrology resulting from anthropogenic disturbance. Sedimentation rates of agricultural depressions greatly exceed depressions surrounded by grasslands and can reduce wetland storage capacity and hydroperiod (Luo et al. 1997; Gleason and Euliss 1998). On the Southern High Plains of Texas, playas surrounded by agriculture were more likely to become inundated than playas in grassland watersheds during the growing season, but were less likely to hold water through the winter (Johnson et al. 2011). This demonstrates that, while playas surrounded by agricultural land-use were more likely to receive run-off, they also had diminished water storage capacity due to sedimentation. Given the agricultural landscape of central Oklahoma, it may be that agricultural-induced sedimentation is impacting the hydroperiod of interdunal depressions. As a result, additional research on land-use effects on sedimentation rates and resultant impacts to wetland hydroperiod in Pleistocene Sand Dune depressional wetlands is necessary.

Rainfall amount, timing and intensity as well as long term drought severity (PDSI) were all good predictors of wetland inundation. In all but the winter, a one cm increase in maximum rainfall had a greater impact on wetland inundation probability than a one cm increase in total rain. These results support the concept that in the semi-arid Southern Great Plains, the largest intensity storm events are critical for generating the infiltration excess runoff necessary to fill surface water-dependent depressional areas (Pilgrim et al. 1988). In arid Australia, Roshier et al. (2001) found that many wetlands were dependent on large infrequent rainfall events and thus, vulnerable to changes in the frequency and magnitude of those events. We found that projected increases in the intensity of the largest spring rainfall events increased the frequency of wetland inundation. However, the effect may be moderated or even reversed in years that begin in extreme drought resulting from the predicted decrease in summer precipitation and increase in temperatures. We found that as drought (measured as PDSI) increased, more rainfall was required to inundate the wetlands in the study region. Since PDSI can be considered a measurement of soil moisture (Szep et al. 2005), our results are intuitive; as drought increases in severity, antecedent soil moisture decreases. Therefore, more precipitation is captured higher in the watershed during all but the largest storm events, and runoff is reduced (Castillo et al. 2003).

The impacts of climate variables on wetland inundation probability in our study generally support the idea that not just rainfall quantity but also rainfall intensity and drought conditions play a role in influencing inundation. Given that future climate projections for central North America include increased storm intensity as well as increased drought severity and intensity (Shafer et al. 2014), it is important that these

variables are included in models used to predict future wetland hydrology. While many regional wetland hydrological models use standard increases for projected total rainfall throughout the course of the year, an advantage of our model is that we can also observe how changes to the size and timing of the most intense storms impact wetland inundation probability. These predictions should be viewed as preliminary, which can be refined in the future as we gain more accuracy in precipitation projections from regionally downscaled climate models. However, these models currently lack certainty in precipitation patterns (Zhang et al. 2011), particularly for the most extreme events (Sunyer et al. 2012) critical for driving the hydrology of the wetlands in our study area.

While the modeling approach used for this study has several advantages (e.g., freely available data, regional approach with site specific variables, and incorporation of rainfall intensity and drought variables), the negative rainfall coefficients in summer and winter requires that the model be refined to make future inundation predictions outside of the spring. The negative rainfall coefficients appear to be caused by two factors: the manner in which seasons were divided and the relatively long interval between Landsat images. In the summer, the majority of inundation events (54%) occurred in June when total rainfall and evaporation were relatively low compared to late summer images. On average, a wetland would have experienced 15.5 cm less evaporation for the three months prior to June compared with the three months prior to August (NOAA 1982). Therefore, grouping June inundation events with the spring may provide greater accuracy for summer month coefficients. Although total rainfall is likely to be less important in summer due to the evaporative potential of the summer months, the coefficient is potentially underestimated due to the long interval between Landsat scenes. It is possible

that some wetlands became inundated and dried during summer intervals and thus, were incorrectly considered dry in the model. It is likely that integrating additional sources of satellite imagery and running the model for a longer time period may increase the availability of shorter duration image pairs.

Despite the current limitations of the model outside of the spring season, we believe that this approach could prove useful in regions that contain high densities of depressional wetlands where the detailed data necessary to create deterministic models are lacking and cost-prohibitive. Using only freely available data to both identify wetland inundation and predict wetland inundation are advantageous in both the time and cost of model development. Furthermore, by integrating local and landscape variables associated with individual wetlands within the region, we are able to not only determine regional changes to wetland hydrology but also determine which wetlands are most susceptible to climate change induced impacts. Under increased drought scenarios, the numerous small wetlands in the region will be susceptible to decreased inundation frequency, altering the spatial arrangement of available inundated habitat, with potential implications for the numerous taxonomic groups that rely on the hydrologic dynamics (Jeffries 2011, Chase 2007), connectivity (Ishiyama et al. 2014) and density of wetlands (Albanese et al. 2012). Thus, it will be critical to understand the drivers of wetland inundation to develop conservation plans to mitigate climate induced hydrological alterations. Moving forward, we plan to continue to refine the model and test in other regions in the Southern Great Plains that contain high densities of wetlands.
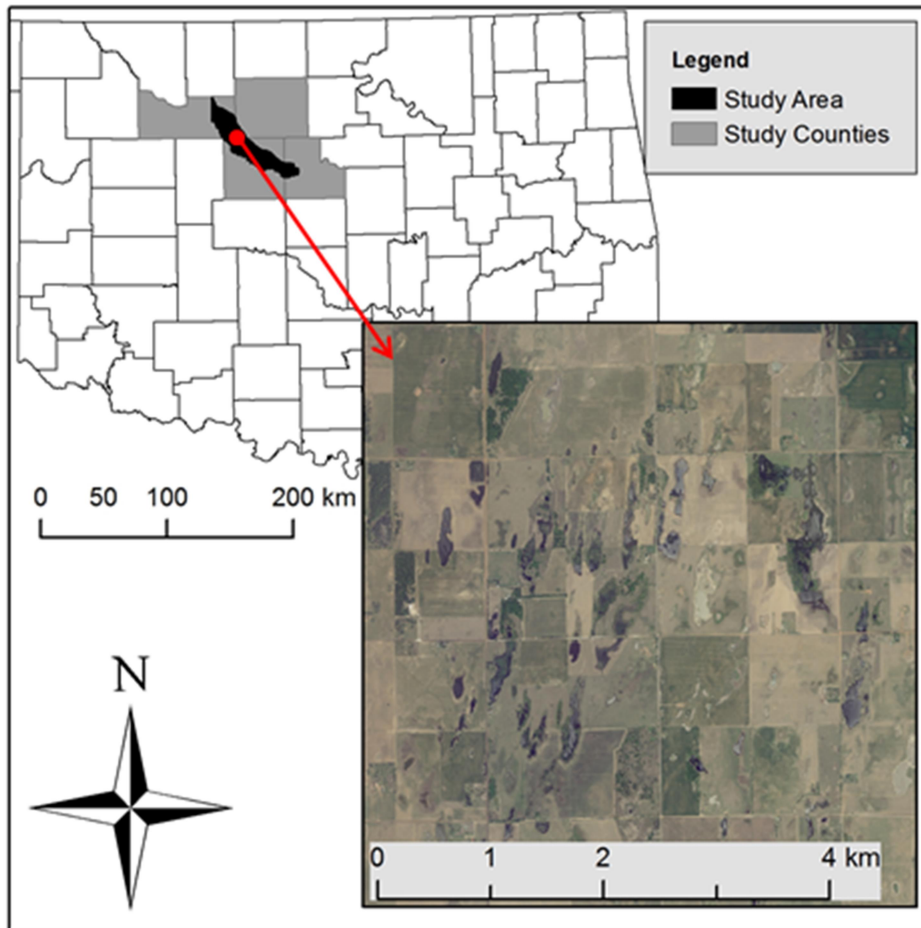
ACKNOWLEDGEMENTS

Fig 1 Map of the study area in the Cimarron River Pleistocene Sand Dunes Ecoregion of central Oklahoma and aerial image of a portion of the study area highlighting a location of high wetland density

(a)

(b)

(c)

(d)

(e)

(f)
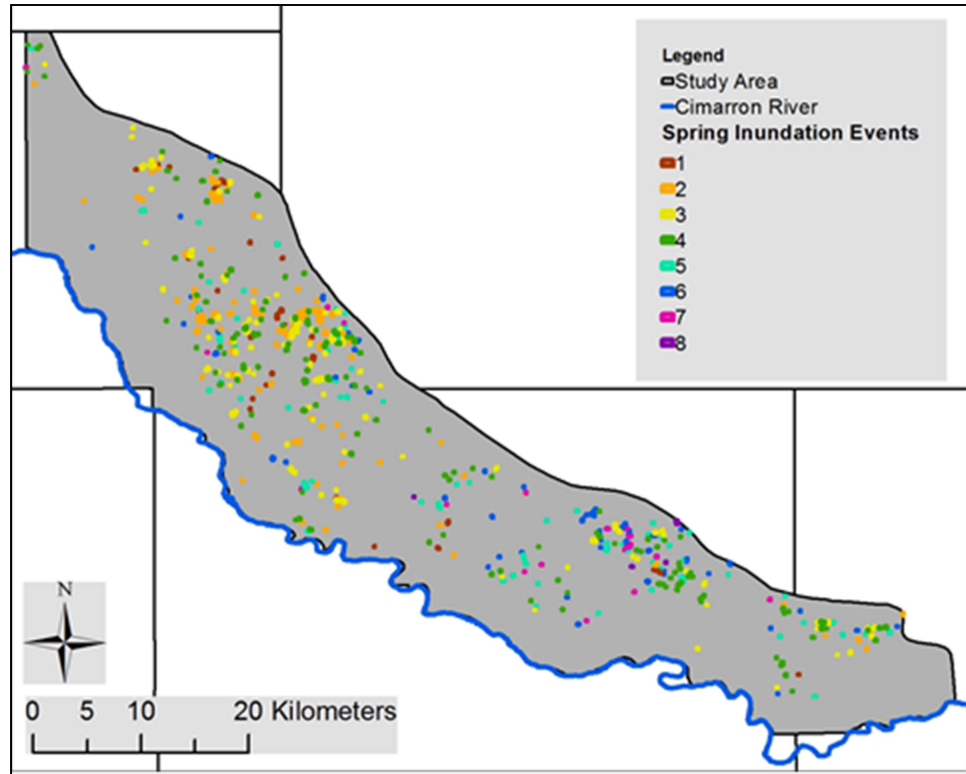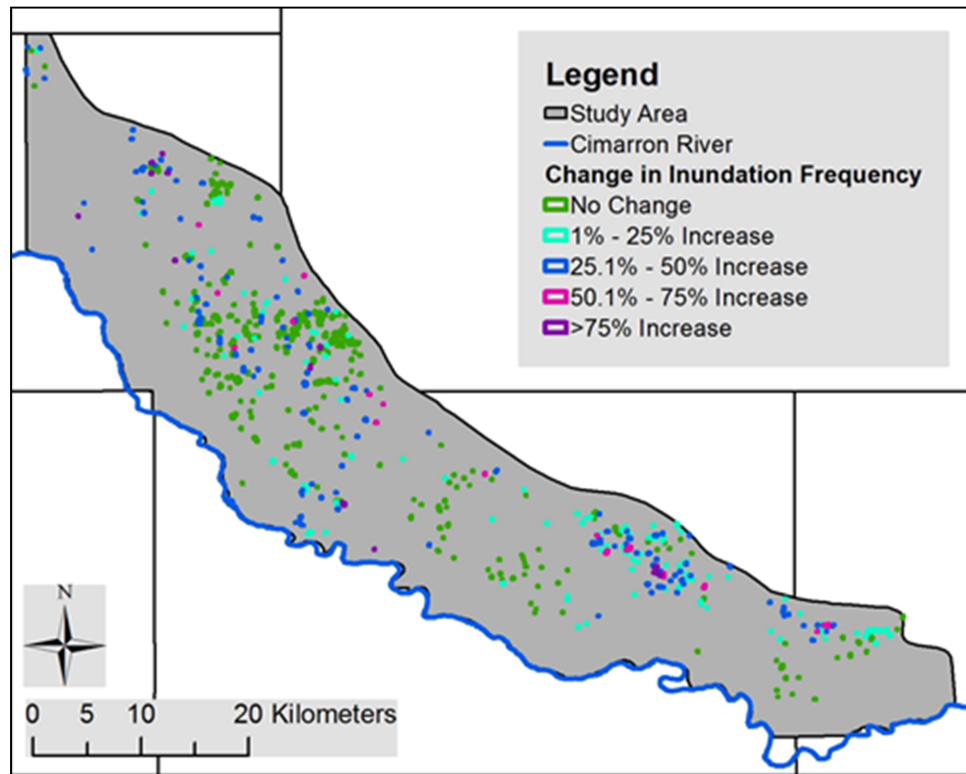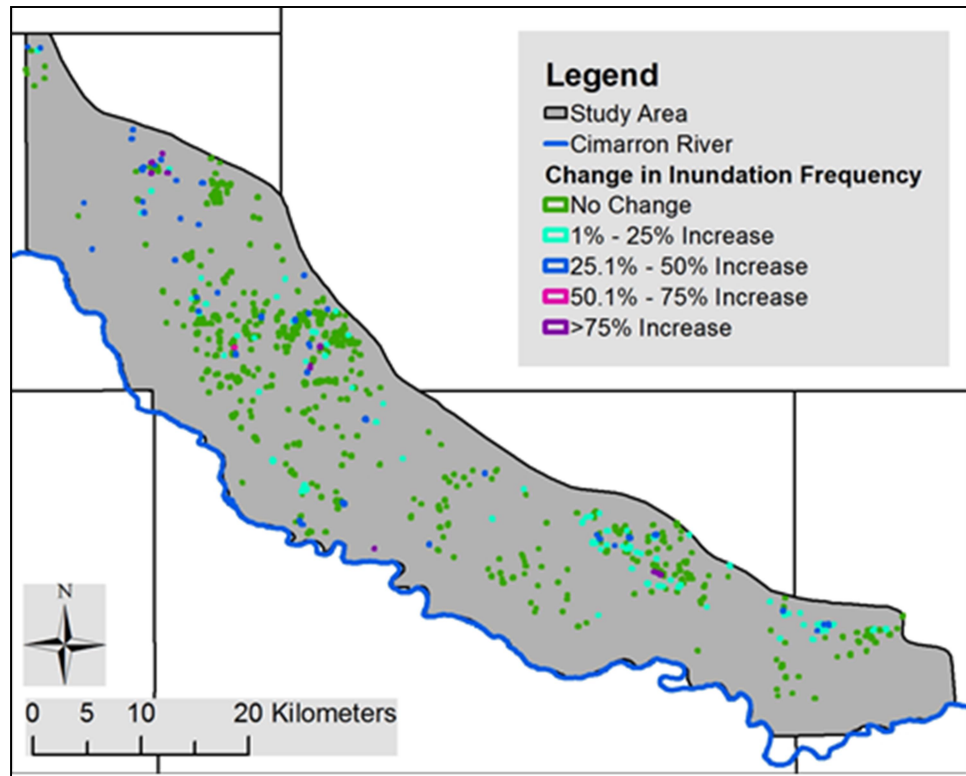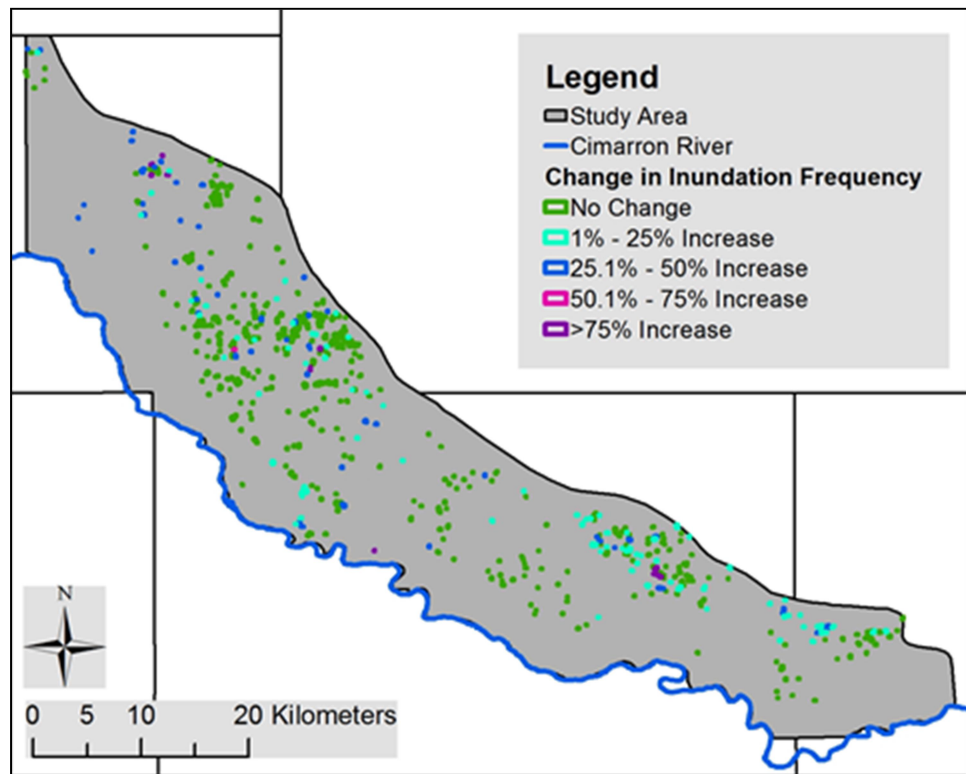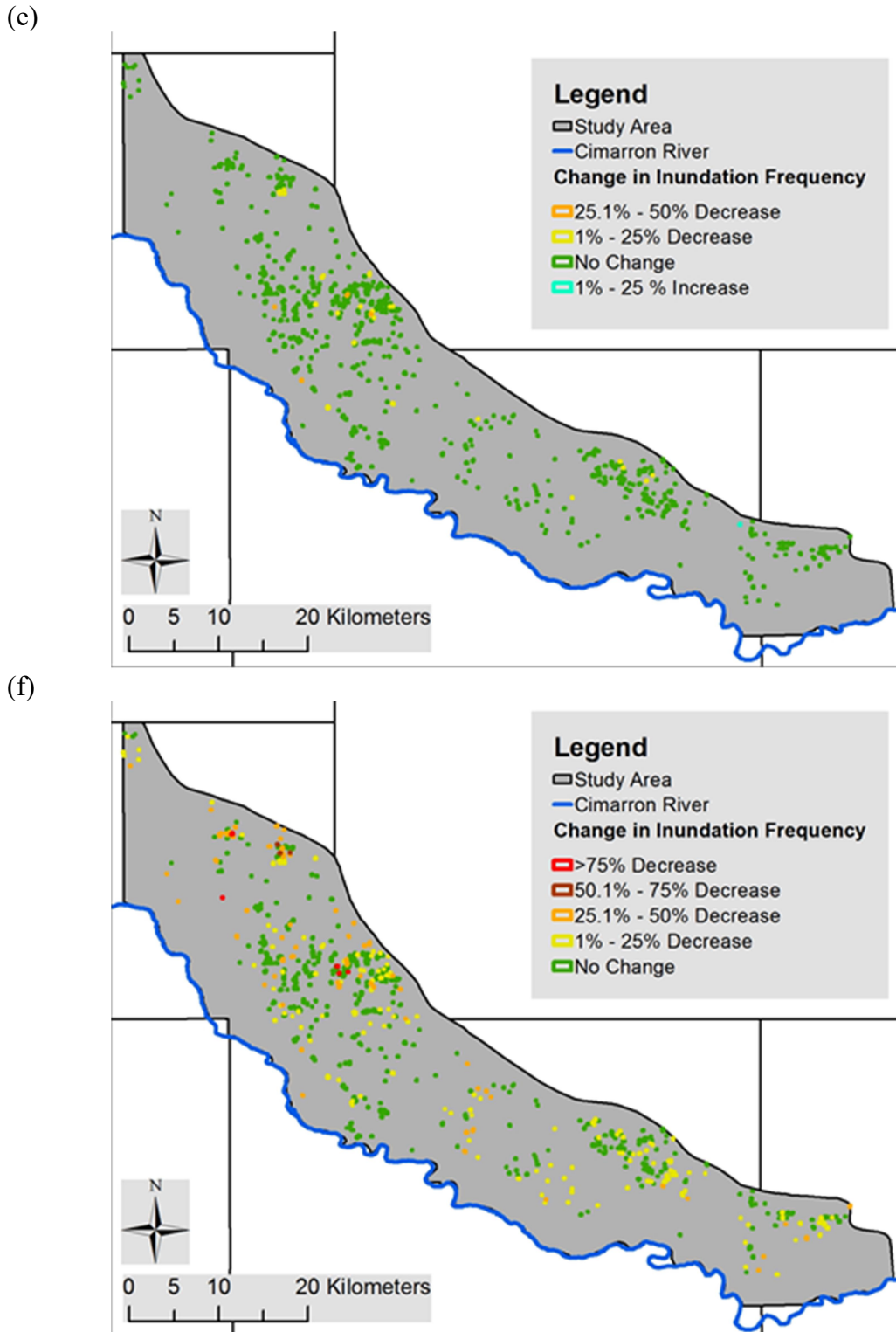
Fig 2 (a) Number of spring inundation events for the 497 wetlands included in the inundation model for depressional wetlands in the Cimarron River Pleistocene Sand Dunes Ecoregion of central Oklahoma. Change in the frequency of inundation events for each wetland under scenarios (b) +MAX (c) +TOT (d) +MAX-PDSI (e) +TOT-PDSI and (f) -PDSI

(a)
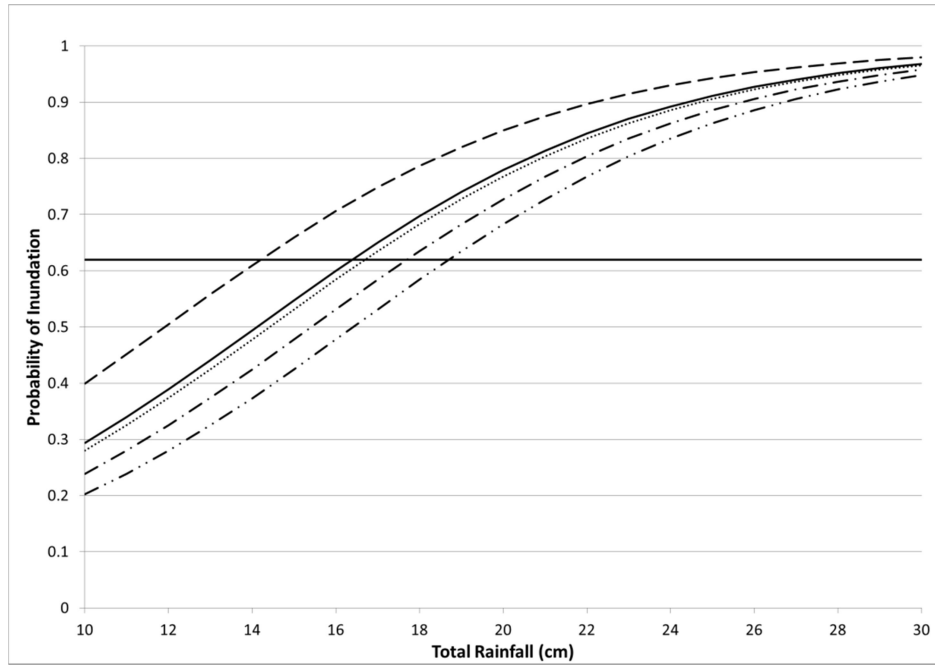
(b)
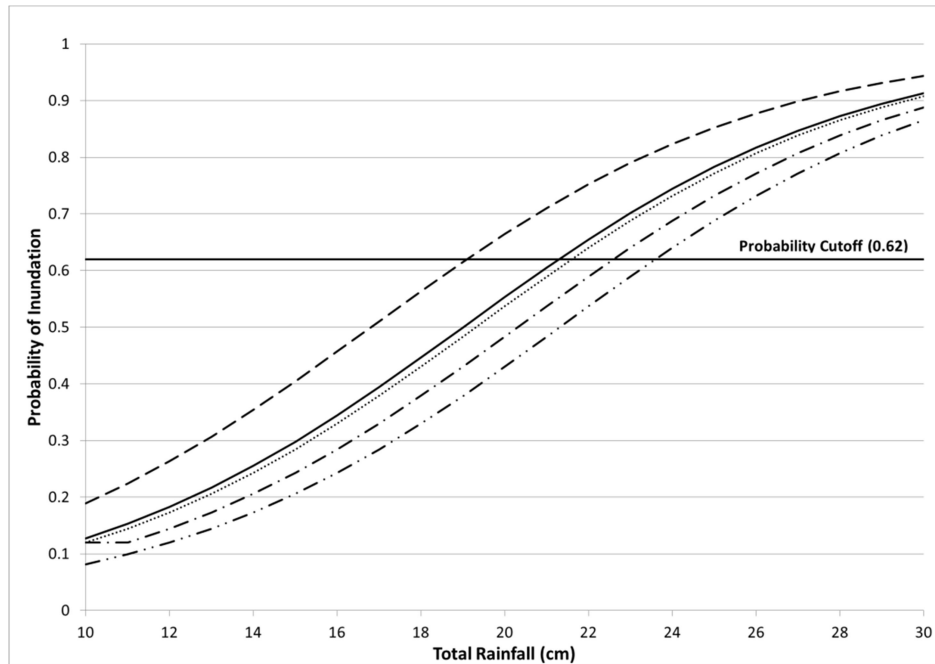
Fig 3 (a) Probability of inundation of a 3 hectare agricultural wetland under variable total spring rain in the Pleistocene Sand dunes of Central Oklahoma with 4.5 cm max rain and 0 PDSI (solid line), 6.1cm max rain and 0 PDSI (dashed line), 6.1 cm max rain and -2.5 PDSI (dotted line), 6.1 cm max rain and -3.5 PDSI (dash-dot line) and 6.1 cm max rain and -4.5 PDSI (dash-dot-dot line). Probability cutoff of 0.62 determined by maximizing kappa statistic of model validation dataset. (b) Probability of inundation of a 0.4 hectare grassland wetland under variable total spring rain. Lines represent the same scenarios as (a)

Table 1. Candidate models from AICc model selection for a model used to predict wetland inundation in the Cimarron River Pleistocene Sand Dunes Ecoregion of central Oklahoma. Potential variables included percentage of agriculture in the surrounding watershed (%Crop), average soil drainage class in the surrounding watershed (Drainage), Palmer Drought Severity Index (PDSI) at the start of the sample period, maximum rainfall event for the sample period (Max Rain), total rainfall for the sample period (Total Rain), season, wetland size, watershed size and interaction effects of Max Rain by season and Total Rain by season. + indicates a positive relationship between the variable and wetland inundation, – indicates a negative relationship and y indicates that the variable is included. Interactions between rainfall variables and season are denoted as Max Rain*Season and Total Rain*Season.

%Crop	Drainage	PDSI	Max Rain	Total Rain	Season	Wetland Size	Watershed Size	Max Rain* Season	Total Rain* Season	df	ΔAICc
+	-	+	+	+	y	+	-	y	y	17	0
+		+	+	+	y	+	-	y	y	16	0.69
+	-	+	+	+	y	+		y	y	16	2.39
+		+	+	+	y	+		y	y	15	2.59

Table 2. Independent variables included in the model selected for predicting depressional wetland inundation in the Pleistocene Sand Dunes Ecoregion of the Cimarron River in central Oklahoma from 1995-2011. Associated coefficient values, odds ratios and marginal effects are presented.

Independent Variable	Coefficient	Odds Ratio	Marginal Effect
Intercept (Spring)	-5.60569	0.004	n/a
Winter	-4.33524	0.013	n/a
Fall	-2.66965	0.069	n/a
Summer	-4.31799	0.013	n/a
Total Rain: Spring	0.21403	1.239	0.034
Total Rain: Winter	0.18962	1.209	0.03
Total Rain: Fall	0.01147	1.012	0.002
Total Rain: Summer	-0.06228	0.940	-0.01
Max Rain: Spring	0.31376	1.369	0.05
Max Rain: Winter	-0.29298	0.746	-0.046
Max Rain: Fall	0.12242	1.130	0.02
Max Rain: Sumer	0.57369	1.775	0.091
PDSI	0.21434	1.239	0.034
%Crop	0.43178	1.540	0.069
Wetland Size	0.23701	1.267	0.037

Table 3. Percentage of study depressional wetlands inundated for maximum and total rainfall amounts under no drought (0 PDSI) and extreme drought conditions (-5 PDSI) in the Pleistocene Sand Dunes Ecoregion of the Cimarron River in central Oklahoma in the spring.

| | Maximum 24 Hour Rain (cm) | | | | | | | | | | | |
| | 2 cm | | 4 cm | | 6 cm | | 8 cm | | 10 cm | | 12 cm | |
Total Rain	0 PDSI	-5 PDSI	0 PDSI	-5 PDSI	0 PDSI	-5 PDSI	0 PDSI	-5 PDSI	0 PDSI	-5 PDSI	0 PDSI	-5 PDSI
12 cm	0%	0%	1%	0%	1%	1%	8%	1%	81%	2%	100%	13%
14 cm	1%	0%	1%	0%	3%	1%	34%	1%	100%	7%	100%	40%
16 cm	1%	0%	2%	1%	16%	1%	94%	3%	100%	32%	100%	100%
18 cm	1%	1%	8%	1%	83%	2%	100%	15%	100%	91%	100%	100%
20 cm	3%	1%	40%	1%	100%	8%	100%	82%	100%	100%	100%	100%
22 cm	17%	1%	95%	3%	100%	36%	100%	100%	100%	100%	100%	100%
24 cm	85%	2%	100%	17%	100%	93%	100%	100%	100%	100%	100%	100%
26 cm	100%	9%	100%	84%	100%	100%	100%	100%	100%	100%	100%	100%
28 cm	100%	44%	100%	100%	100%	100%	100%	100%	100%	100%	100%	100%
30 cm	100%	97%	100%	100%	100%	100%	100%	100%	100%	100%	100%	100%
32 cm	100%	100%	100%	100%	100%	100%	100%	100%	100%	100%	100%	100%

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CHAPTER III

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SPATIOTEMPORAL VARIABILITY AT LOCAL AND REGIONAL SCALES: IMPACTS ON

WETLAND INVERTEBRATE COMMUNITIES

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Abstract: In highly dynamic ecosystems such as wetlands, it is likely that local (e.g. competition, vegetation structure) and regional (immigration) effects vary spatiotemporally. Seasonal hydrologic cycles impact the physicochemical environment and niche availability within a wetland. At the regional scale, wet and dry periods can alter the spatial arrangement of available inundated habitat, causing fluctuations in the dispersal rates between wetlands. We assessed the impacts of local vegetation complexity and wetland connectivity on the richness and metacommunity organization of invertebrates in temporarily flooded depressional wetlands in central Oklahoma, with a focus on how effects change seasonally and between years. We found evidence that both vegetation complexity and wetland connectivity affect wetland invertebrate communities and that the relationships varied temporally. Vegetation complexity has a greater effect on richness and sites with similar vegetation increase in community similarity at the end of the growing season. Dispersal appears to be primarily driven by distance to permanently flooded wetlands and ponds that function as refuges during periods of drought. Early in the season, dispersal increases wetland richness and makes proximate sites more compositionally similar. Late in the season, the spatial scale at which wetlands are connected appears to depend on the number of inundated wetlands regionally. During dry periods, when fewer wetlands are inundated, proximate wetlands become more similar (~10 km). During wet periods, wetland similarity increases at

broad scales (~ 100 km). Understanding the temporal fluctuations in local and regional effects is likely to elucidate the complex patterns of wetland invertebrate community organization. Furthermore, we suggest that in aggregations of temporary wetlands, maintaining permanently inundated ponds and wetlands may be critical in sustaining invertebrate communities.

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INTRODUCTION

Despite the abundance of studies on invertebrate communities in wetlands (e.g. Meyer et al. 2015, Kneitel 2014, Bischof 2013, Davis et al. 2006, Batzer et al. 2004, Tangen et al. 2003), broadly applicable concepts on the factors controlling community dynamics have been elusive (Batzer 2013). In fact, many studies have often concluded that weak relationships exist between wetland invertebrates and a variety of environmental factors (Meyer et al. 2015, Tangen et al. 2003). Furthermore, the response of wetland invertebrates to these factors tends to be highly variable between regions and through time (see Batzer 2013 for a review). The lack of clear relationships between wetland invertebrates and environmental factors has led some to hypothesize that freshwater wetland invertebrates are primarily composed of generalists adapted to the dynamic environment that they inhabit (Batzer et al. 2004). In other words, unpredictable patterns of inundation (i.e., timing, frequency and duration) cause spatiotemporal variability in the physicochemical environment (Baldwin and Mitchell 2000) and habitat complexity (Deil 2005), promoting invertebrate taxa tolerant of variable environmental conditions.

Batzer (2013) proposed the alternative concept that wetland invertebrate communities, rather than primarily comprised of generalists, are responding to complex interactions among multiple environmental factors. In this scenario, the same factor may cause different responses in the invertebrate community depending upon the other environmental conditions at that place and time. Highlighting these potentially complex relationships, Meyer et al. (2015) found that richness, diversity and the abundance of the most common invertebrate taxa were impacted by differing contributions of local, landscape and temporal factors. Dynamic interactions between local biotic (e.g., competition and predation), local abiotic (e.g., water quality and vegetation structure) and regional factors (e.g., immigration and extinction) may contribute to the spatially and temporally variable invertebrate community responses observed in wetlands. However, studies of the factors influencing wetland invertebrate communities, like most traditional ecological studies, have focused primarily on local factors as the determinants of community structure (Chase and Leibold 2003). Regional factors (i.e., dispersal) are also a critical aspect of community organization in wetlands (Williams 1996, Williams 1985) because natural dry periods in hydrologic cycles effectively eliminate habitat for obligate aquatic invertebrates. The ability of a community to reassemble following inundation is dependent on emergence of taxa with a desiccation resistant stage and colonization from external habitats (Fraaije et al. 2015, Sim et al. 2013, Wiggins et al. 1980).

Recently the focus has shifted towards integrating regional factors with local factors in community ecological studies (Liebhold and Gurevitch 2002). While, the importance of regional factors in shaping ecological communities dates back to the theory of island biogeography (MacArthur and Wilson 1967), development of the

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metacommunity theory has reemphasized that communities are not spatially closed (Leibold et al. 2004, Hubbell et al 2001). Metacommunities are a set of local communities that interact with communities in surrounding habitats through dispersal (Leibold et al. 2004). In an analysis of over 150 datasets, Cottenie (2005) found 37% of the metacommunities evaluated were influenced by spatial arrangement of the component habitat patches, indicating the importance of accounting for dispersal dynamics in studies of community structure. Additionally, in wetland specific studies, connectivity between wetlands has been shown to increase invertebrate community similarity (Cottenie et al. 2003) and within wetland richness (Ishiyama et al. 2014). Furthermore, taxa with greater dispersal ability tend to have more homogenous communities over broader scales (Patrick et al. 2014).

The influence of dispersal on metacommunity organization is dependent on the ability of the constituent organisms to move through the environment and colonize new patches (Borthagaray 2015, Moquet and Loreau 2003), and the degree to which local factors act as an environmental filter to remove poorly adapted colonists (Chase 2007). In cases when dispersal rates are low, it is likely that local environmental filtering dominates community structure. Habitat patches that are heterogeneous in the local factors that differentially influence survival among species will create heterogeneous communities between locales (Leibold et al. 2004). In this scenario, low rates of immigration from surrounding habitats do not effectively replace poor local competitors. When dispersal rates are high, the explanatory power of within wetland environmental gradients will likely be reduced. In a heterogeneous environment, regionally good competitors can persist at specific locations where they are poor competitors because

frequent immigration can counteract local extinction (Moquet and Loreau 2003). In extreme cases, dispersal rates may be so great that community homogenization occurs at regional scales (Moquet and Loreau 2003, Forbes and Chase 2002).

Due to the potential effects of dispersal from surrounding habitats, landscape connectivity to regional wetlands may be critical in accounting for local community composition patterns (Ishiyama et al. 2014 Patrick et al. 2014, Cottenie et al. 2003). A complicating factor is the temporal variability in connectivity of highly dynamic ecosystems such as wetlands, and subsequent variability in dispersal rates (Datry et al. 2015). Temporary loss of inundated wetlands under drought conditions can alter the spatial arrangement of available patches (Wright 2010). As a region shifts from a period of higher precipitation to drought, the distance between inundated wetlands may increase, which may reduce the ability of organisms to disperse between patches. Several recent studies provide evidence that temporal variability can impact metacommunity dynamics through effects on dispersal patterns (Fraaije 2015, Erős et al. 2014, Langenheder et al. 2012). We expect that as connectivity between wetlands changes over time, the relative importance of local and regional effects on invertebrate communities will also change.

An additional confounding factor in studies of regional and local factors on metacommunities is the disparate life histories of component taxa (Patrick et al. 2014, Pandit et al. 2009, Van de Meutter 2007, Urban 2004). For example, aquatic macroinvertebrates vary greatly in their ability to move between geographically isolated habitats (Vieira et al. 2006, Bohonak and Jenkins 2003), and as such, different taxa may perceive the same landscape as fragmented or connected (Borthagaray et al. 2015). Borthagaray et al. (2015) assessed the scales of habitat connectivity relevant for aquatic

invertebrates, and found greater site occupancy when using connectivity thresholds between ponds ranging from 500 to 1500 m depending on the taxonomic order. Further, organisms that use different dispersal strategies appear to be differentially influenced by regional factors. Organisms that utilize active dispersal strategies (e.g., taxa that can move between habitats without assistance) are generally influenced more by regional effects than those species that utilize passive dispersal strategies (e.g., taxa that rely on wind, water or animal transport) (Cottenie et al. 2005). Because wetland invertebrate communities are generally composed of organisms that use both strategies, studying subsets of the community independently may be necessary to understand how local and regional effects structure metacommunities. However, studies of actively and passively dispersing pond invertebrates have found variable relationships between dispersal strategy and regional effects (Van de Meutter et al. 2007, Urban 2004). These contrasting findings indicate that regional differences in spatial arrangement and degree of direct connectivity between ponds likely cause dispersal to vary in importance in structuring invertebrate communities.

In this study, we evaluate the factors influencing active and passive disperser communities of temporary depressional wetlands of central Oklahoma. We assess seasonal and yearly variability in local and regional effects on metacommunity organization, as well as the spatial scales at which dispersal operates. While most metacommunity studies focus on similarity in community composition between sites or β-diversity, we also wanted to determine the spatial and temporal scales at which connectivity affects within wetland richness or α-diversity. This provides insight into not only the relative importance of dispersal in affecting community composition but also

how the spatial arrangement of habitat patches influences rates of movement. For local factors, we focus on wetland vegetation complexity because in a previous regional study, Meyer et al. (2015) found that vegetation structure was the most important local factor in influencing wetland communities.

METHODS

Study area

The study area includes portions of the Pleistocene Sand Dunes Ecoregions of central Oklahoma adjacent to the Cimarron and Salt Fork of the Arkansas (Salt Fork) Rivers (Omernik 1987). Aeolian dune fields have formed on the leeward terraces of the Cimarron and Salt Fork Rivers during periods of extreme drought. The last period of dune mobilization occurred along the Cimarron River approximately 800-900 years ago. Within the now stabilized dune fields, a large number of depressional wetlands occur throughout the interdunal valleys (Lepper and Scott 2005). The area averages a density of 4 wetlands per sq. km but upwards of 20 per sq. km occur in some locations (Dvorett et al. 2016*)*. The majority of wetlands are small (<0.5 hectares), surface water-fed systems that are erratically flooded (50% of years on average) due to highly variable precipitation patterns in the semi-arid Southern Great Plains. Additionally, the majority of wetlands have temporary hydroperiods that typically last less than half the growing season (Dvorett et al. 2016) because evapotranspiration greatly exceeds precipitation in the region (Oklahoma Mesonet 2015). As a result, distances between wetlands can fluctuate dramatically within and between years.

Invertebrate and vegetation sampling

We sampled a total of 44 wetlands that were located in three clusters: Kingfisher County (KIN), Major/Garfield Counties (MAJ) and Grant County (GRT). KIN (13 sites) and MAJ (14 sites) are located in the Cimarron Dunes and GRT (17 sites) occurs in the Salt Fork Dunes (Fig. 1). Wetlands within a cluster were < 10 km apart and distances between clusters were approximately 30 km, 60 km, and 75 km between KIN and MAJ, MAJ and GRT, and KIN and GRT, respectively. We sampled invertebrates and vegetation complexity during the early (29 March through 15 May) and late growing seasons (15 June through 26 July) in 2009 and 2010. In 2009, we sampled 19 sites (5 in MAJ and 14 in GRT) and in 2010, 37 sites (10 in GRT, 13 in KIN and 14 in MAJ).

We collected invertebrate samples at each site using the Quadrat-Column-Core (QCC) method, which combines vegetation quadrat, water column and benthic core samples. QCC effectively samples epiphytic, nektonic and benthic communities (Meyer et al. 2013). At each site, we collected 5 QCC samples when only one vegetation stratum (submergent, emergent, or open water) was present and 6 samples when two strata were present (3 samples per stratum). Each QCC sample consisted of a 50 X 50 cm quadrat of clipped vegetation (DeCoster and Persoone 1970, Anderson and Smith 1996), two 5.2 cm diameter water column samples (Swanson 1978, Anderson and Smith 1996) and one 5.2 diameter benthic core sample (Swanson 1983). Samples were processed using standard protocols according to Meyer et al. (2015) and we identified invertebrates to genera, when possible (Merritt et al. 2008, Smith 2001). All samples at a site from each sample date were aggregated to calculate species richness. Each species was also placed into a dispersal strategy category of passive or active dispersers (Merritt et al. 2008, Vieira et al. 2006). Passive dispersers are those taxa that rely on other animals or wind for movement

between disconnected wetlands and were represented primarily by Branchiopoda and Gastropoda taxa (Urban 2004). Active dispersers can move between wetlands without aid, and were dominated by insects with flight ability. We also scored vegetation complexity (VC) at each sample location from 1 (e.g., chairmaker's bulrush [*Schoenoplectus americanus*]) to 3 (e.g., southern waternymph [*Najas guadalupensis*]) based on the degree of structural complexity and branching of the species present. Vegetation complexity was then averaged for all samples at a site for a given sample date.

Connectivity effects on within wetland community

To test the effects of wetland connectivity on α-diversity of invertebrates within a wetland, we compared taxa richness to twelve connectivity metrics described in Table 1. We calculated the connectivity metrics for each wetland in ARCGIS 10.1 (ESRI, Redlands, California) using Landsat (USGS 2015) images that were classified to identify all inundated water pixels. Classification of water and upland pixels was completed using decision tree analysis according to methods outlined in Dvorett et al. (2016*)*. Classifications had a high level of accuracy as indicated by kappa > 0.93. Kappa is a measure of observed classification accuracy compared with the expected accuracy. Kappa values greater than 0.8 are considered an excellent classification (Landis and Koch 1977). A wetland was considered available habitat if it had at least one pixel of water classified in a Landsat scene.

Some metrics quantified connectivity between available wetland habitats at the time of sampling (short-term) and others quantified average connectivity (long-term). Connectivity metrics were assessed at different temporal resolutions because aquatic

invertebrates utilize spatial dispersal through colonization and temporal dispersal through diapause. Therefore, colonization may occur within a season or over multiple years with desiccation resistant life stages stored in the sediment (Bilton et al. 2001). The wetlands with greater connectivity over long time periods may accumulate more desiccation resistant taxa, and the taxa present at the time of sampling may represent dispersal events from previous years. For metrics that calculated connectivity at the time of wetland sampling, we used a concurrent Landsat scene collected close to the date of invertebrate collection (20 April for Early 2009, 24 June for Late 2009, 23 March for Early 2010 and 13 July for Late 2010). For metrics that calculated long-term wetland connectivity, we used a wetland map that aggregated an 18 year dataset of 51 Landsat images (Dvorett et al. 2016).

Metrics were characterized into six categories to assess if and how spatial and/or temporal connectivity impact invertebrate richness. The six categories included: (1) Nearest, (2) Buffer, (3) Short-term Graph, (4) Long-term Graph, (5) Short-term Temporal, and (6) Long-term Temporal. Each category included two connectivity metrics. The first four categories are measures of spatial connectivity but represent different potential mechanisms for dispersal. "Nearest" connectivity metrics included distance to nearest semi-permanent or permanent wetland (DSPW) and area of the most proximate wetland (ADSPW). These metrics assess if colonization from source sites with longer hydroperiods influence the richness at temporary wetlands. "Buffer" metrics included the number of wetlands (BW) as well as the number of semi-permanent and permanent wetlands (BSPW) in a 1 km radius circle. These metrics assess if invertebrate richness increases in more densely aggregated wetlands through multidirectional

dispersal. We calculated "Buffer" and "Nearest" metrics from long-term wetland maps.

We also measured spatial connectivity using a graph theory approach using concurrent

Landsat (Short-term Graph) and long-term wetland maps (Long-term Graph). Graph

theoretical approaches allow for quantification of the spatial arrangement of habitat

patches that acknowledges the dispersal ability of organisms. Graph theory represents

suitable habitat patches as nodes that are linked through edges. The distance at which

nodes are considered linked can be adjusted to represent the ability of organisms to move

through the landscape. An aggregation of collected nodes is called a component (Urban

and Kiett 2001).

Using a 1 km connectivity threshold, we calculated component size (CS) and the

decrease in the Integral Index of Connectivity (dIIC) (Ishiyama 2014, Pascual-Horta and

Saura 2006) using Conefor 2.6 (Saura and Torné 2009). CS is simply a measure of the

number of connected nodes within a component. IIC is a measure of both the distance

between and area of connected units within a component (Eq. 1). dIIC is the loss in IIC

when a particular habitat patch (i.e., wetland) is lost (Eq. 2) (Pascual-Horta and Saura

2006).

(1) $\text{IIC} = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} a_i \, X \, a_j/(1+nl_{ij})}{A_L^2}$

(2) $\text{dIIC}_k(\%) = \frac{\text{IIC} - I_{\text{remove,k}}}{\text{IIC}} \, X \, 100$

Where, i and j are two wetlands within the component, a is the area of wetlands i and j,

A_L is the total area of wetlands within each cluster (15 km radius circle) and nl is the

distance between wetlands i and j. Additionally, k is a wetland that is removed from a

component to calculate the resultant loss in connectivity (IIC) following removal

Because IIC measures between patch distances, it can be computationally prohibitive,

when patch number becomes large. As a result, we limited quantification of graph metrics to a 15 km radius circle that encompassed all wetlands within a cluster. Figure 2 represents examples of these metrics.

The last four metrics measured hydrologic persistence or temporal connectivity within a study wetland at the time of sampling (Short-term Temporal) and average conditions (Long-term Temporal). We assessed temporal connectivity because persistence of inundated conditions has the potential to increase invertebrate richness by increasing the time available for colonization. We quantified inundation length (IL) by observing the number of consecutive Landsat scenes when the wetland contained water, prior to sample collection. We used three Landsat scenes per year (spring, summer, and fall). Drought length (DL) was quantified in a similar manner by observing the number of consecutive Landsat scenes when a wetland remained dry, prior to the most recent inundation event. Average hydroperiod (AvgHy) and frequency of inundation (FREQ) were attained from the long-term wetland map developed by Dvorett et al. (2016).

We used a linear model selection approach (Burnham and Anderson 2002) to identify relationships between invertebrate species richness and the twelve wetland connectivity variables using the package BBMLE (Bolker 2016) in program R (R Core team 2013). We completed model selection separately for all pairwise combinations of time of sampling (early vs. late) and dispersal strategy (active vs. passive) and considered all models with Delta Akaike Information Criteria (ΔAICc) less than two as candidate models (Akaike 1974). Each model selection included 19 possible candidate models. For each of the six metric categories (i.e., Buffer, Short-term Graph), we included all three combinations of the two metrics within the category (i.e., Buffer models include:

BW+BSPW, BW, BSPW) as well as the null model. In addition to testing for regional (connectivity) effects on invertebrate richness, we assessed the seasonal variation in local (vegetation complexity) effects on active and passive disperser richness using linear regression. These analyses were conducted separately from the connectivity model selection.

Connectivity effects on metacommunity dynamics

To test for the importance of regional (dispersal) and local (vegetation complexity) effects on invertebrate metacommunity dynamics, we ran a series of analyses using the package Vegan (Oksanen et al. 2016) in program R (R Core team 2013). To test for similarity in invertebrate community by distance between wetlands, we ran partial Mantel tests (Mantel 1967) on the Sørenson Dissimilarity Index, which uses taxa presence/absence data (Sørenson 1948). If dispersal is an important influence on community composition, we would expect proximate wetlands to have more similar communities than distant wetlands. Vegetation complexity was used as a covariate to account for any distance effects resulting from potential similarity in vegetation structure of adjacent wetlands. Since the Mantel test does not provide information on the spatial scale at which communities are correlated, we used Welch's t-test (Welch 1947) to compare within year changes to community similarity by distance. For each pair of wetlands, the early year Sørenson Index was subtracted from the late year Sørenson Index, and wetland pairs were divided into two groups for analysis: within cluster (wetlands in the same cluster) and between cluster (wetlands in two different clusters).

We used permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) to assess the effects of local (vegetation complexity) and regional (cluster) factors

on community similarity. Terms were added sequentially to PERMANOVA, with vegetation complexity added first to account for similarity of sites within a cluster due to potential similarity in vegetation structure. To assess the degree of similarity of invertebrate communities within clusters, we used a multivariate analysis of group dispersions (PERMDISP) using the function Betadisper, which tests differences in average distance to a group centroid with a permutation-based significance test. PERMDISP can be considered a test of β-diversity within a region (Anderson et al. 2006). For all permutation tests, we used 9999 iterations. To determine how regional (e.g., distance, cluster) and local (vegetation complexity) factors may vary temporally in their ability to structure metacommunities, partial Mantel tests, PERMANOVA, and PERMDISP were run on all pairwise combinations of year, time of sampling, and dispersal strategy

RESULTS

Connectivity effects on richness

Active disperser richness increased with decreasing distance to the nearest semi-permanent wetland in the early season. The variation explained was small (adj. R^2 of 0.07), and by the end of the growing season, the null model was similar in likelihood to any of the connectivity models. This indicates that the effect of DPSW on active dispersers is reduced as the season progresses (Table 2). The best models for passive dispersers in the early season included increased richness with closer proximity to the nearest semi-permanent wetland and increased values of WIIC (greater connectivity). However, the relationships were weak and the null model was also among the best models. By the end of the season, passive disperser richness was best explained by the

component size at the time of sampling, indicating greater late season richness for wetlands in more connected landscapes. Vegetation complexity explained much more variation in invertebrate richness than any connectivity metrics, particularly for active dispersers (Table 3). Active disperser richness increased with greater vegetation complexity in both the early season (R^2=0.23) and the late season (R^2=0.55). Passive dispersers had a similar relationship with vegetation complexity in the early season (R^2=0.23), but the explained variance was reduced by the end of the growing season (R^2=0.19).

Connectivity effects on metacommunity dynamics

Active disperser community similarity by distance varied by time of year and the results differed between years (Table 4). Correlation by distance for active dispersers increased in 2009 (0.23 to 0.53) and decreased in 2010 (0.26 to - 0.07). The results of Welch's t-test on change in Sørenson index indicate that the late 2009 increase in similarity by distance was due to both an increase in within cluster similarity and a decrease in between cluster similarity. Contrarily, in 2010, both within and between cluster similarity increased but was significantly greater for sites in different clusters (Table 5). Cluster effects in the PERMANOVA followed a similar trajectory with greatest variance explained in late 2009 (R^2=0.13) and early 2010 (R^2=0.14). This indicates that the differences in community composition were greatest between clusters during late 2009 and early 2010. Results of the PERMDIST also indicate that clusters exhibited differences in β-diversity. In late 2009 and late 2010, GRT wetlands were more similar than MAJ wetlands. We found no difference in variance between clusters in the early season of either year. GRT county wetlands seemed to increase in similarity as the

growing season progressed, while KIN and MAJ sites maintained relatively constant β-diversity. Vegetation complexity effects on community similarity, like effects on within site richness, increased late in the growing season. In other words, sites with similar vegetation structure were generally more similar in community composition throughout the study, but the effect was strongest in the late season. In general, VC explained more variance in community similarity than wetland cluster, except in early 2010 (R^2=0.11 and R^2=0.14, respectively).

Passive dispersers exhibited similar patterns as active dispersers, but distance, cluster and VC generally explained less variation in community similarity (Table 4). Passive disperser community was only significantly correlated with distance between wetlands in late 2009 (0.41). Despite an increase in community similarity by distance in 2009, both within cluster sites and between cluster sites decreased in similarity late in the season but distant sites became even more dissimilar than proximate sites (Table 5). In 2010, both within and between cluster sites increased slightly in similarity and there was no significant difference between the groups. Like active dispersers in the PERMANOVA, cluster explained the most variation in the passive disperser community in early 2010 (R^2=0.12). However, unlike active dispersers, VC explained the most variation in the passive disperser community in early 2009 (R^2=0.26).

DISCUSSION

Regional and local effects on active dispersers

Our results demonstrate that both local (VC) and regional (wetland connectivity) factors impact within wetland richness and metacommunity organization of wetland invertebrates. Furthermore, the relative importance of local and regional factors varied

seasonally and between years. For active dispersers, we found evidence that wetlands and ponds with more permanent hydroperiods act as a source of colonists to wetlands with ephemeral and temporary hydroperiods early in the growing season. It is well documented that aquatic invertebrates without a desiccation resistant stage rely on refugia provided by permanent waters during periods of drought (Svensson 1999, Wiggins et al. 1980, Williams 1977). In semi-arid playa wetlands, similar to wetlands included in this study, the majority of the invertebrate community is comprised of insect taxa that colonize from surrounding playas and irrigation pits with longer hydroperiods (Anderson and Smith 2004). However, there has been little assessment of the effects of proximity to permanent "refuge" ponds on rates of recolonization at temporary wetlands (Wilcox 2001). The results of our study suggest that proximity to source wetlands may increase the rate of recolonization early in the year, though DSPW explained a relatively small amount of variation in community richness. This is not surprising given that seasonal colonization is not the only mechanism by which wetlands accumulate invertebrate taxa. The taxa present during sampling may have persisted in the soil through desiccation resistance (Bilton et al. 2001), or colonized in previous years in cases where the site remained inundated for long periods (Tarr et al. 2005). Furthermore, while certain generalist taxa may be influenced by connectivity of wetlands, other habitat specialists may be primarily influenced by local environmental factors (Pandit et al. 2009).

By the end of the summer, connectivity had little effect on active disperser richness. There are likely two reasons for the reduction: (1) given more time, dispersing invertebrates can reach wetlands farther from source populations and (2) local factors had a greater effect on invertebrate communities as the season progressed. Our results

provide evidence for seasonal changes in dispersal limitation and increased

environmental filtering late in the growing season. Firstly, the results of our community

similarity analyses provide support for seasonal homogenization resulting from dispersal.

In 2009, proximate wetlands become more similar and in 2010, wetlands across the entire

study area become more similar as the season progressed. Seasonal homogenization of

the actively dispersing component of the invertebrate metacommunity is well

documented for clusters of wetlands and has been attributed to lack of dispersal

limitations (Vanschoenwinkel et al. 2010, Moorhead et al. 1998). For example,

invertebrate communities inhabiting playa wetlands in the Southern High Plains of the

United States became more similar as the year progressed due to aerial colonization of

insect predators (Moorhead et al. 1998). Fairchild et al. (2003) found permanent

wetlands supported greater richness in beetle assemblages, but by the end of the growing

season, temporary and permanent sites supported similar richness due to dispersal

between closely aggregated ponds.

In addition to the seasonal increase in community similarity, we found that

regional effects were variable in their spatial influence between years. In 2010, clusters

of wetlands became more similar late in the year and the change was primarily due to

increasing similarity of distant wetlands. However, in 2009 we found increased

similarity by distance because wetlands within a cluster become more similar and distant

wetlands decreased in similarity. We hypothesize that between year differences in our

study may be a response to landscape level changes in the arrangement of available

inundated wetland habitat. In central Oklahoma, 2009 represented the culmination of an

extremely wet period that began in 2007 (Mesonet 2015). The summer of 2009 was then

relatively dry, and approximately 60% of the wetlands inundated within our study

clusters in April were dry by July (Table 6). Contrarily, in 2010, the number of wetlands

remained relatively constant from spring to summer (~4% increase). As a result, the

decrease in community similarity between clusters in late 2009 may be a result of

decreased wetland connectivity and subsequent dispersal limitation. Whereas, in 2010,

sufficient connectivity was likely present to allow for dispersal and homogenization

(Figure 3). To our knowledge, no study has directly correlated temporal changes in

landscape connectivity with shifts in the relative importance of regional effects on

wetland invertebrate metacommunities. However, Alexander et al. (2012) found that

when connectivity was altered due to habitat fragmentation, spatial effects became more

important in structuring plant metacommunities. Additional research directly quantifying

relationships between landscape connectivity and wetland invertebrate metacommunity

organization using long-term datasets will help to illuminate between year variability in

regional effects we found in this study.

In our study, active disperser richness and community similarity were more

strongly related to VC than any connectivity metric. VC has long been suggested to

increase the richness and abundance of aquatic invertebrates (Krull 1970, Krecker 1939)

by offering refuge from predators (Diehl 1992), oviposition sites, increased food sources

and available habitat (Heck et al. 1977). In central Oklahoma wetlands, vegetation

structure was the most important local factor affecting invertebrate community

composition (Meyer et al. 2015). The relationship, however, appears to be more complex

with specific feeding guilds responding more favorably to complex vegetation structure

and others increasing in less densely vegetated habitats (Meyer et al. 2015, Hornung and

Foote 2006, Murkin et al. 1992). For example, Hornung and Foote et al. (2006) found that herbivores were more abundant in complex vegetation while collector-filterers and predators were less abundant. Our results indicate that the importance of VC in structuring invertebrate communities is also influenced by season, as we found a stronger relationship with richness and increased community similarity as the season progressed in both 2009 and 2010. While the mechanism for the weaker early season relationship between vegetation complexity and invertebrate community is unknown, it is possible that early season dispersal may play a role. High rates of early season colonization from surrounding wetlands may reduce the influence of vegetation structure on invertebrate communities.

This study suggests that attempts to quantify relationships between local factors and actively dispersed invertebrate communities will be improved by understanding the temporal variability in both local and regional effects (Datry et al. 2015). Though, it is difficult to conclusively determine that spatial similarity is due to dispersal and not by unaccounted for spatially autocorrelated environmental factors (Cottenie et al. 2005). In this study, we only quantified variation associated with vegetation complexity because of its known importance in structuring invertebrate communities regionally. Other factors such as water quality and hydrology also impact regional wetland invertebrate communities (Meyer et al. 2015). However, the early season connectivity effects on richness we identified lend support to the fact that dispersal is indeed impacting early season metacommunity. Furthermore, we believe the between year variation in late season similarity by distance effects are best explained by changes in connectivity of wetlands. The scale at which dispersal operates late in the year appears to be dependent

on the number of inundated wetlands on the landscape. During dry periods, it appears that wetlands in close proximity are more similar than distant wetlands, and during wet periods dispersal can operate to increase community similarity over broad scales. If spatially autocorrelated local factors were impacting the observed distance-based community similarity, it is more likely that we would have detected similar patterns in both late 2009 and late 2010.

Regional and local effects on passive dispersers

Rates of passive dispersal are generally considered low (Bohonak and Jenkins 2003) and most passive dispersers persist in dry wetlands using dormancy (Brock et al. 2003). As a result, we expected that passive dispersal richness would be more closely related to length of inundation. Furthermore, studies of passively dispersing invertebrates have found that direct hydrologic connections between wetlands and ponds leads to similarity in the invertebrate community, but that hydrologically-disconnected systems are primarily influenced by local environmental factors (Van de Meutter et al. 2007, Cottenie et al. 2003). However, it appears in our study area that dispersal does play a role in passive disperser community organization but the relationships are less clear. Connectivity effects increased for passive dispersers as the year progressed. Late in the year, wetland richness was best explained by the component size (number of connected wetlands with a connectivity threshold of 1 km) at the time of sampling. This is contrary to the early connectivity effects of nearest permanent wetland on active dispersers. Passive dispersers appear to rely on movements between densely clustered wetlands, likely because most taxa are desiccation resistant (Brock et al. 2003) and do not require permanent wetlands as refugia. The increase in connectivity effects as the season

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progressed may be a result of the time needed for emergence of desiccation resistant stages. The cues for dormancy breakage are complex (Brock et al. 2003) and can be related to temperature and photoperiod (Anderson and Smith 2004). Anderson and Smith (2004) found most taxa broke diapause between three and nine weeks following inundation. Therefore, early season samples may have been collected prior to the emergence and potential movement between proximate wetlands.

Our results suggest that wetland connectivity may influence passive dispersal on relatively short time scales and at broad spatial scales. For example, Louette and DeMeester (2005) found evidence that passive dispersers (cladocerans) can rapidly colonize newly constructed ponds. Within eight months, the ponds had been colonized by an average of two species of Cladocera and the species richness at the ponds was affected by the richness of regional water bodies within 3 km (Louette and DeMeester 2005). That said, in our study, the passive disperser community generally had weaker similarity by distance relationships than the active community. Furthermore, when similarity by distance increased in late 2009, it was not because of increase in similarity of close sites. Rather, sites within a cluster grew dissimilar late in the year but distant sites grew significantly more dissimilar. Therefore, the spatial effects on passive dispersers in our study are likely operating at regional scales. Other studies have found regional spatial effects on passive dispersing invertebrates (Shurin et al. 2001, Declerck et al. 2011). For example, in High-Andes temporary wetlands, invertebrate communities were primarily determined by environmental factors at small spatial scales (Declerck et al. 2011). However, regional factors become more important when comparing communities at broad scales between valleys (Declerck et al. 2011).

At fine spatial scales, movement of passive dispersers may be virtually unlimited given long enough temporal scales because most taxa can persist in dry wetlands through diapause or desiccation resistance. In closely aggregated ponds, Urban (2004) concluded that overland movement did not pose a significant barrier to passive dispersers. Since certain taxa of zooplankton are known to persist in dry soils for nearly 200 years (Bilton et al. 2001), they can maintain diapause until environmental conditions are appropriate for emergence (Brock et al. 2003). As a result, even in circumstances where dispersal rates are low (Bohonak and Jenkins 2003), the taxa present at a given time are potentially a result of dispersal over long periods. Therefore, it may only be at larger spatial scales that movement between suitable habitats is constrained (Declerck et al. 2011)

Connectivity metrics and spatial scale

In assessing the effects of connectivity on communities, it is critical to quantify the landscape in a manner and scale that captures the ability of organisms to disperse between habitats. Simple patch-based connectivity metrics have been criticized by Kadoya (2009), due to their inability to quantify the landscape in a biologically meaningful manner. However, in highly fragmented landscapes with relatively small habitat patches, it has been predicted that distance becomes the best measure of connectivity due to random movement of organisms (Kadoya 2009, Hanski 1999). Even in these highly fragmented landscapes, nearest neighbor has been deemed inferior to other metrics because it ignores patches that are potentially within dispersal distance (Bender et al. 2003, Moilanen and Nieminen 2002). But, in our study, nearest neighbor was the best measure of wetland connectivity for active dispersers. The DSPW metric appears to be conceptually grounded to dispersal mechanisms and thus, explains a real

biological phenomenon (i.e., recolonization of temporary wetlands from permanent wetlands). In a metanalysis of invertebrate colonization studies, Prugh (2009) found that nearest neighbor metrics performed as well as other patch based metrics when the distance was calculated to the nearest occupied patch, rather than simply the nearest patch. Distance based measurements have the additional advantage that no prior knowledge of the dispersal threshold is required (i.e. buffer radius; Prugh 2009). Therefore, in disconnected wetlands, distance-based metrics may be a suitable option for measuring connectivity when the source populations can be identified reliably. In this study, the source populations appear to be wetlands with longer hydroperiods.

Conclusions

We found that metacommunity organization within an extremely dynamic wetland complex was affected by temporally and spatially variable local and regional factors. We hypothesize that regional differences and local temporal variation in environmental factors that shape and drive invertebrate communities are likely influenced by the spatial configuration of suitable habitat patches as well as the change in that configuration over time. Attempts to use biotic communities in wetlands for assessment of ecosystem health have often been confounded by the lack of consistent environment-community relationships (Euliss and Mushet 2011, Tangen et al. 2003, Wilcox et al. 2002). Understanding the spatial and temporal scales over which communities fluctuate may be critical to developing regionally-relevant assessments of wetland condition. For example, when transient taxa were identified and removed from analyses, wetland odonate communities exhibited clearer metacommunity classification (Bried et al. 2015a) and stronger responses to environmental gradients (Bried 2015b).

This study also provides evidence that maintenance of invertebrate metacommunities in semi-arid depressional wetland regions may depend on sustaining relatively rare wetlands with longer hydroperiods. In our study area, semi-permanent and permanent wetlands comprise less than 5% of the total wetland population, but appear to be important refuges for taxa that lack desiccation resistance. Drought is a harsh environmental filter that can greatly reduce regional biodiversity (Chase 2007), and external recolonization is a critical factor in invertebrate community assemblages (Wiggins et al. 1980). In central Oklahoma, projections for longer periods of drought and intervals between rainfall events (Shafer et al. 2014) may increase drought stress and reduce the number of refuges available for aquatic invertebrates and alter wetland connectivity. Continued study of wetland connectivity on invertebrate persistence and dispersal rates will be critical to our understanding of the drivers of local and regional invertebrate diversity as well as the development of empirically-based conservation strategies.

ACKNOWLEDGEMENTS
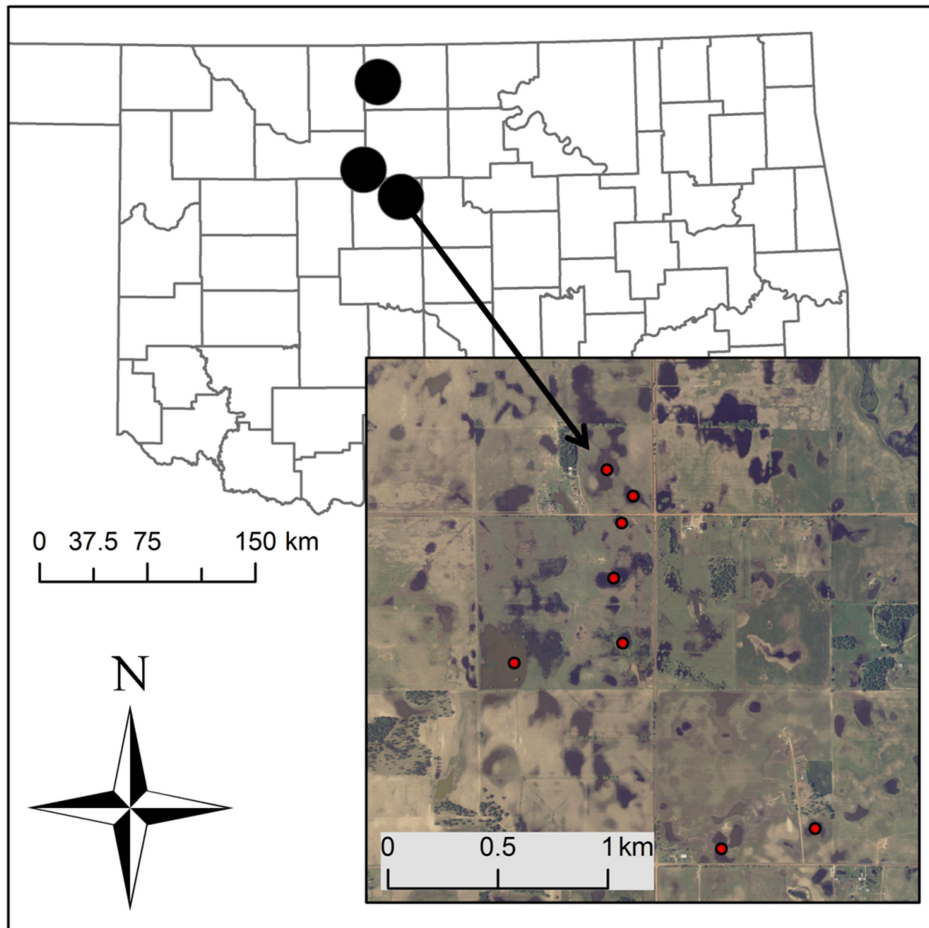
Figure 1. Study area for the assessment of local and regional effects on invertebrate communities of central Oklahoma depressional wetlands in 2009 and 2010. Each black circle represents a wetland cluster. An aerial image from 2008 highlights a portion of the Kingfisher wetland cluster, with red circles representing wetlands included in the study.
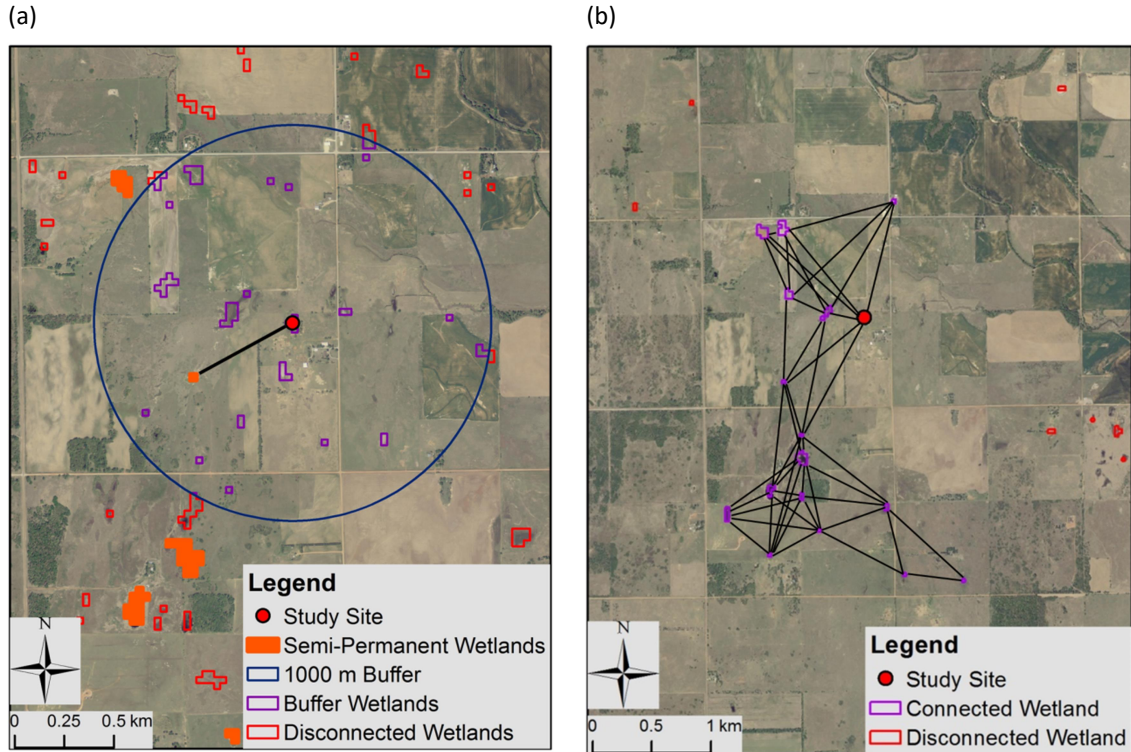
Figure 2. (a) An example of nearest neighbor and buffer metrics calculated to assess connectivity effects on invertebrate communities of central Oklahoma depressional wetlands (Grant County). The black line represents the Euclidian distance to the nearest semi-permanent wetland from a study site. Purple wetlands represent sites within a 1 km buffer and included in buffer metrics. (b) An example of a wetland graph constructed using a 1 km connectivity threshold. Black lines represent edges connecting wetland nodes < 1 km apart.
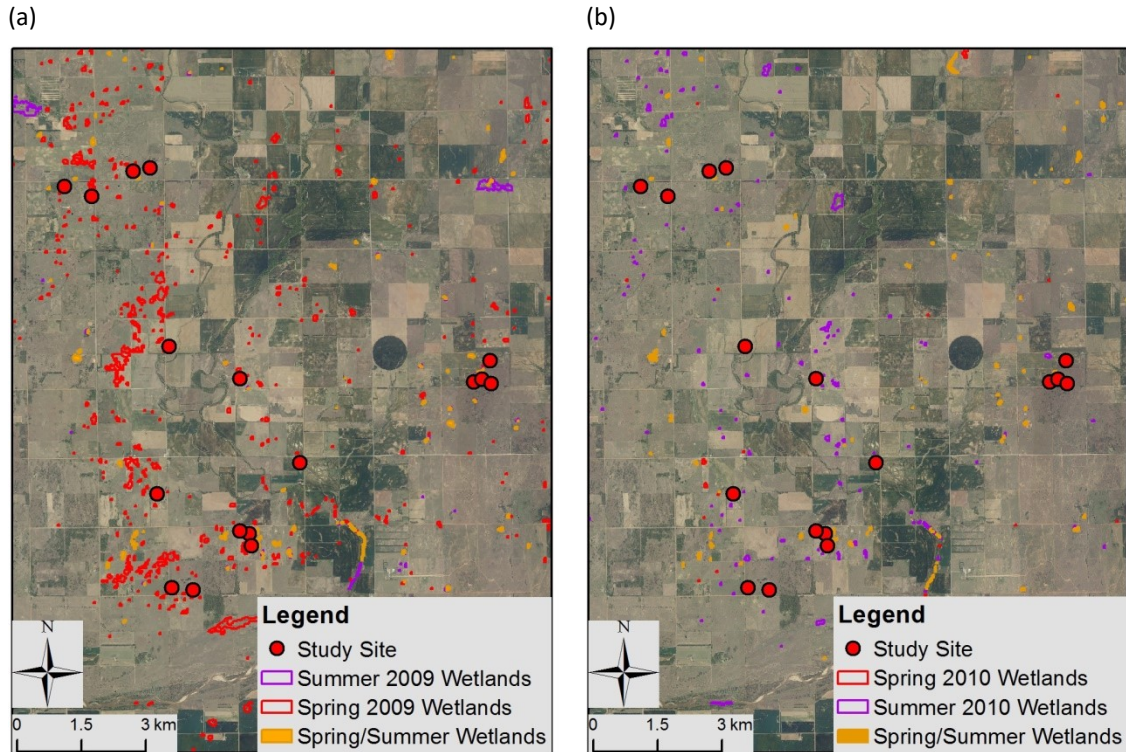
Figure 3. Inundated Grant County, Oklahoma wetlands in (a) 2009 and (b) 2010 demonstrating variability in inundated wetland distribution during the course of this study. In 2009, the region was wet in the spring but many wetlands were dry by the summer. In 2010, the region was relatively wet in the spring but contained more inundated wetlands by the summer.

Table 1. List of the twelve connectivity metrics used in the model selection of invertebrate species richness at depressional wetlands in central Oklahoma. The twelve metrics were divided into six metric types (two metrics per type), which represented competing models in the analyses.

| Metric Category	Metric Name	Metric description
Nearest		
	DSPW	Euclidian distance to nearest semi-permanent or permanent wetland (m)
	ADSPW	Area of nearest semi-permanent or permanent wetland (ha)
Buffer		
	BW	Number of surrounding wetlands in a 1 km radius circle
	BSPW	Number of surrounding semi-permanent wetlands in a 1 km radius circle
Graph: Short-Term		
	LIIC	Decrease in the Integral Index of Connectivity using a 1 km connectivity threshold and concurrent Landsat imagery
	LCS	Number of wetlands in a connected component using a 1 km connectivity threshold and concurrent Landsat imagery
Graph: Long-Term		
	WIIC	Decrease in the Integral Index of Connectivity using a 1 km connectivity threshold and wetland map
	WCS	Number of wetlands in a connected component using a 1 km connectivity threshold and wetland map
Temporal: Short-Term		
	IL	Length of inundation prior to sampling
	DL	Length of drought prior to last inundation event
Temporal: Long-Term		
	AVGHY	Average hydroperiod determined from wetland map
	FREQ	Average frequency of inundation determined from wetland map

Table 2. Results of the model selection of invertebrate richness in central Oklahoma depressional wetlands in the early (a) and late (b) growing seasons of 2009 and 2010. Model selections were run on active and passive disperser communities separately. Explanatory variables in the candidate models with ΔAICc < 2 include nearest semi-permanent or permanent wetland (DSPW), area of the nearest semi-permanent or permanent wetland (ADSPW), Integral Index of Connectivity using a Landsat derived wetland map (WIIC), the number of semi-permanent or permanent wetlands in a 1 km radius circular buffer (BSPW), component size of the Landsat derived wetland map (WCS) and component size of the concurrent Landsat image (LCS).

(a) Early

	Model Variables						Adj. R^2
Dispersal Group	DSPW	ADSPW	WICC	BSPW	ΔAICc	Weight	
Active Dispersers							
M1: Nearest	-0.005				0	0.28	0.07
M2: Nearest	-0.005	-0.17			1.7	0.12	0.06
Passive Dispersers							
M1: Nearest	-0.001				0	0.11	0.03
M2: Graph: Long-Term			0.9		0.3	0.1	0.03
M3: Buffer				0.3	0.6	0.08	0.02
M4: Null					0.7	0.08	

(b) Late

	Model Variables				Adj. R^2
Dispersal Group	WCS	LCS	ΔAICc	Weight	
Active Dispersers					
M1: Graph: Long-Term	0.004		0	0.12	0.02
M2: Null			0.2	0.11	
Passive Dispersers					
M1: Graph: Short-Term		0.008	0	0.67	0.15

Table 3. Results of regression analysis testing the effects of vegetation complexity on invertebrate species richness of central Oklahoma depressional wetlands for the early growing season (29 March through 15 May) and late growing season (15 June through 26 July) in 2009 and 2010. Analyses were run for active dispersers and passive dispersers separately.

Dispersal Category	Coefficient	R^2	p-value
Early Active Dispersers	3.2	0.23	0.0001
Early Passive Dispersers	1.23	0.23	0.0001
Late Active Dispersers	5.94	0.55	<0.0001
Late Passive Dispersers	1.11	0.16	0.001

Table 4. Results of the partial Mantel tests, PERMANOVA and PERMDISP for (a) actively dispersing and (b) passively dispersing invertebrates of central Oklahoma wetlands for four time periods (early 2009, late 2009, early 2010 and late 2010). Partial Mantel tests included vegetation complexity (VC) as a covariate and we provide Pearson's ρ and p-value. We used PERMANOVA with VC and wetland cluster (CL) as independent variables. PERMDISP was run on wetland clusters, Major (M), Grant (G) and Kingfisher (K). Cluster dispersions are presented (M, G, and K) along with p-values for pairwise comparisons between clusters (M-G, M-K, and G-K).

(a) Active dispersers

| | Partial Mantel Test | | PERMANOVA | | | | PERMDISP | | | | | |
| | | | Veg. Complex. | | Cluster | | Cluster | | | p-value | | |
Period	ρ	p-value	R^2	p-value	R^2	p-value	MAJ	GRT	KIN	M-G	M-K	G-K
early 2009	0.23	0.04	0.11	0.03	0.07	0.2	0.48	0.41	n/a	0.26	n/a	n/a
late 2009	0.53	0.002	0.19	0.001	0.13	0.007	0.55	0.35	n/a	0.01	n/a	n/a
early 2010	0.26	0.0001	0.11	0.001	0.14	0.001	0.48	0.47	0.43	0.69	0.14	0.27
late 2010	-0.07	0.84	0.21	0.001	0.07	0.07	0.47	0.31	0.43	0.03	0.56	0.06

(b) Passive dispersers

| | Partial Mantel Test | | PERMANOVA | | | | PERMDISP | | | | | |
| | | | Veg. Complex. | | Cluster | | Cluster | | | p-value | | |
Period	ρ	p-value	R^2	p-value	R^2	p-value	MAJ	GRT	KIN	M-G	M-K	G-K
early 2009	0.1	0.19	0.26	0.004	0.05	0.29	0.27	0.19	n/a	0.39	n/a	n/a
late 2009	0.41	0.006	0.14	0.05	0.06	0.35	0.48	0.26	n/a	0.02	n/a	n/a
early 2010	0.03	0.26	0.05	0.14	0.12	0.03	0.27	0.23	0.22	0.38	0.19	0.68
late 2010	-0.01	0.52	0.13	0.001	0.1	0.04	0.26	0.19	0.18	0.21	0.15	0.94

Table 5. Results of Welch's t-test comparing seasonal change in Sørenson for wetland pairs within a cluster and between a cluster. Negative values indicate that the invertebrate community of a wetland pair have become more similar. Analyses were run separately for active and passive disperser communities of central Oklahoma depressional wetlands in 2009 and 2010.

	Change in Sørenson Index		
	Within Cluster	Between Cluster	p-value
2009			
Active Dispersers	-0.06	0.07	<0.0001
Passive Dispersers	0.12	0.24	0.0006
2010			
Active Dispersers	-0.05	-0.12	0.0001
Passive Dispersers	-0.03	-0.04	0.72

Table 6. The number of wetlands in each of the study clusters (Major, Grant and

Kingfisher) and a circular region encompassing all the study areas with a 60 km radius in

central Oklahoma.

	Number of Inundated Wetlands			
Period	Major	Grant	Kingfisher	Region
Early 2009	662	1528	651	54,949
Late 2009	311	544	334	41,572
Early 2010	665	541	1207	72,071
Late 2010	842	748	908	57,455

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