Past, present, and future landscape changes in the Southern Great Plains:
Effects of urbanization and energy extraction on the playa network

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ABSTRACT

The Great Plains of North America are an iconic expanse of arid and semi-arid prairies, grasslands, and steppes that occupy much of the North American continental interior. Within the Southern High Plains (SHP, the southern-most extension of the Great Plains), patterns of energy extraction practices and urbanization have induced several land-use/land-cover changes that have altered ecological processes of embedded ecosystems. For regional aquatic ecosystems, these alterations are manifest across a network of ephemeral, runoff fed wetlands know as playas. Playas are regional centers of biodiversity, are integral to Ogallala Aquifer recharge, and have been incorporated into urban settings as sites of recreation and stormwater management. However, playas face increasing challenges to their functionality due to on-going expansion of the linked factors of energy extraction and urbanization. Furthermore, these challenges are magnified by climatic shifts. Addressing these concerns, and playa ecology in general, is complicated by playa abundance, spatial distribution, and by extensive private land ownership. Thus, this dissertation serves to investigate how each of these drivers of ecological change through time (from recent historical periods, to near present, and into the future) have or are likely to influence playa network functionality, using integrated GIS and remote-sensing techniques, thereby by-passing in-situ constraints. The overall goal of this dissertation is to augment our understanding of how landscape ecological patterns mediate ecological processes. Ultimately, these studies aim to inform regional land use and conservation management of wetlands in areas of expanding energy extraction practices and urban development across local, regional, and global scales.

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CHAPTER I

OVERVIEW OF THE GREAT PLAINS OF NORTH AMERICA AND DISSERTATION RESEARCH CONTEXT.

Introduction

The Great Plains are an expanse of arid and semi-arid prairies, grasslands, and steppes that occupy approximately 1.4-1.9 million km^2 of the North American continental interior (Samson & Knopf, 1994; Wishart, 2004). Characterized by water scarcity (Dodds, Gido, Whiles, Fritz, & Matthews, 2004; Salley, Sleezer, Bergstrom, Martin, & Kelley, 2016; Woodhouse & Overpeck, 1998) (which delayed settlement and even now limits growth), the Great Plains landscape is at the heart of the American national identity, and understanding why and how it was settled is necessary to understand and manage its past, current, and projected future prospects.

Despite numerous classification schemes, no universal consensus of a Great Plains border exists, with definitions based on geomorphological, ecological, anthropogenic, or managerial criteria (Kotkin, 2012; Lewis, 1962; Licht, 1997; Omerick, 2004; Rossum & Lavin, 2000; Webb, 1931; Wishart, 2004). Additionally, the borders of the Great Plains are fluid through time with respect to policy, ecology, climate, and sociology (Lewis, 1962; Rossum & Lavin, 2000). However, the Great Plains are generally considered to be between the Rocky Mountains to the west, eastward to the Mississippi River. They spread northward to fringe the taiga near the Saskatchewan River and extend southward toward the Pecos River, merging into the Chihuahuan Desert (Fig. 1.1).

The Great Plains are not a homogeneous unit, with the northern, central, and southern portions differing in terms of geomorphology, climatic regimes (Borchert, 1950; Lauenroth, Burke, & Gutmann, 1999; Wishart 2004), and settlement patterns (Lewis, 1962; Luebke, 1977). The relatively recent (2 mya) geologic histories of the northern and central portions of the Great Plains share similarity based on continental glaciation events. During the same time period, the geology of the southern portions of the Great Plains were dominated by deposition in the absence of glaciation (Wishart, 2004). The northern, central, and southern portions of the Great Plains also differ in average rainfall and number of frost-free days, as the Great Plains landscapes become progressively drier east to west, and warmer north to south (Borchert, 1950; Lauenroth et al., 1999; Webb, 1931; Wishart, 2004).

Ecologically, the Great Plains can be further divided into three ecological sub-regions, defined by different heights and abundances of dominant grass species (Anderson, 2006; Risser, 1981): tallgrass prairie, mixed-grass prairie, and shortgrass prairie (Mac, Opler, Haecker, Doran, 1998; Samson and Knopf, 1994; Samson and Knopf, 1996). In tallgrass prairie, plant heights historically exceeded 1.5 m, in contrast to the shortgrass prairie, where plant heights averaged <0.3 m. The mixed-grass prairie situated in between typically contained plant heights between 0.3 m and 0.6 m (Fig. 1.1). With the onset of human settlement, the tallgrass region was the first to experience development, with the most arid southern portions of the Great Plains experiencing the most recent large-scale land conversion and development (Licht, 1997; Webb, 1931; Wishart, 2004).

The first human occupants of the Great Plains were prehistoric Native American

peoples (Meltzer, 1999; Vehik, 2014; Wedel, 1972); radiocarbon dating of material from sites near Dallas, TX, suggests that Native Americans may have lived on the Plains for at least 38,000 years (Wishart, 2004), although radiocarbon dating estimates vary considerably (Vehik, 2014). Early agricultural settlements are estimated to have developed in the Great Plains nearly 2,000 years ago. Over time, several long-distance trade networks were established, running from present-day Illinois to New Mexico and northward to Nebraska (Wishart, 2004). Following the European "discovery" of the New World, the Spanish began to settle in the southern Great Plains during the seventeenth century, followed by subsequent waves driven by different socio-political and economic forces (Allen, 1993). As immigrants came to explore and "tame" a vast, unknown American wilderness, these determined individuals, by choice or coercion, left their familiar surroundings to settle the interior frontier. In so doing, they contacted a landscape largely out of the experience of most other people on earth (Allen, 1993), a landscape for which the English language had no word and had to borrow from the French: prairie (Licht, 1997). French expansion followed during the early 18th century, occurring primarily in the southern and central Great Plains; however, this population was largely limited to nomadic traders. By the late 18th century, English settlement began in the Canadian portions of the Great Plains, with establishment of several large trading companies. However, numbers of English settlers also remained relatively small.

After the American acquisition of the Louisiana Territory in 1803 and several sequential legislative actions to promote westward expansion (e.g. The Homestead Act of 1862), large-scale human settlement of the Great Plains began in earnest

around 1860 and lasted into the early 20th century with several waves of migration, mostly from European sources (Shortridge, 1988).

Resulting from these series of subsequent migrations, both domestic and foreign-born settlers would provide some of the most transformative forces to affect the Great Plains, often at the expense of native cultures (Wishart, 1987; Wishart, 2004). Regardless of source region, settlers who arrived in the Great Plains often held dreams of new farming opportunities, freedom from persecution, and increased personal independence. However, these dreams would only become reality after adapting to the unique ecological challenges of the Great Plains (Bennet, 1990; Hall, 1992; Wishart, 2004). Further adaptations would be fostered by railroad development (Kirby, 1983) and new technological advances (Fite, 1977) that transformed the Great Plains landscape. These large-scale conversions and farming practices set the stage for one of the worst human- made natural disasters to impact the Great Plains, the Dust Bowl, which remains one of the most iconic and enduring symbols of Great Plains (Lockeretz, 1978; McLeman et al., 2014; Riebsame, 1986). Between 1925 and 1930, with increasing population pressures and high wheat prices following World War I, speculative farming practices converted an estimated 2,197,345 hectares of southern Great Plains grasslands to cropland (Wishart, 2004; Worster, 2010). During the Great Depression (1929-1939), vast portions of the southern Great Plains experienced severe and protracted droughts. Although droughts had been well-recognized environmental hazards throughout the Great Plains (Dodds et al., 2004; Salley et al., 2016; Woodhouse & Overpeck, 1998) what set these droughts apart were their coupled effects with regional agricultural

mismanagement practices, which gave rise to expansive dust storms and loss of topsoil. The Dust Bowl affected roughly 311,000 km^2 across Colorado, Kansas, New Mexico, Oklahoma, and Texas, ultimately inducing migration outside the Great Plains. During World War II, several sectors of the Great Plains economy rebounded, spurred by defense spending and wartime production (Wishart, 2004). From the 1950s to 2007, the Great Plains experienced an overall population increase from 4.9 million to 9.9 million people; however, many counties experienced decreasing population because of aging and domestic out-migration (Wilson, 2009). Although the patterns and rationale for continued occupation of the Great Plains have varied throughout time; nevertheless, the Great Plains continues to provide residents and immigrants opportunities for social adaptation and personal resiliency akin to the first pioneers.

The Great Plains region is abundant in natural resources ranging from crops to energy sources; however, given the ecological challenges inherent to the region (i.e., droughts, wildfires) and confrontations with indigenous peoples, this portion of the United States was among the last to experience significant settlement and land conversion (Wishart, 2004), which gives us the unique opportunity to witness still-emerging effects of relatively recent large-scale landscape transformation. Since the middle of the 20th century, there has been intensive agricultural cultivation and energy production, leading to several boom and bust cycles of an export-driven economy (Benirschka & Binkley, 1994; Braun, 2016; Wright & Wimberly, 2013; Zellmer, 2008). The growth and contraction of these economic engines have fostered unique demographic and development patterns in the region and today, the

Great Plains showcases extremes in human population dynamics. For example, many rural areas of the Great Plains are still functional frontier zones with population densities of fewer than two people per square mile, limited access to public services, and ongoing depopulation (Duncan, 2000; Wishart, 2004). Conversely, the Great Plains is also the site of some of the fastest rates of urbanization in the United States, with extensive associated growth in infrastructure. Cities of the Great Plains, such as Denver, CO, and Oklahoma City, OK, are considered some of the fastest-growing places in the United States. In Texas, this trend is highlighted with the large urban centers of Dallas and Fort Worth (Kotkin, 2012; United States Census Bureau, 2015). Despite the recent growth trends seen in portions of the Great Plains, this region has historically been defined overall by sparseness both socially and economically (Wishart, 2004).

Driven by the combined forces of increased agricultural production and energy extraction, unparalleled climatic phenomena instigating several regional crises in water availability and advancing urbanization in some areas coupled with depopulation in others, wildlife and human populations of the region alike are facing challenges. These events have changed the Great Plains landscape in terms of its composition, its configuration, and its connectivity for wildlife.

Especially hardest-hit will be overland dispersers with a limited tolerance of sustained arid conditions, such as amphibians. The Great Plains thus provides an elegant canvas for analysis of contemporary natural and anthropogenic landscape-level processes and their subsequent

alteration of ecological pattern-process relationships. At the southern terminus of the Great Plains, the Southern High Plains (SHP) exemplifies the challenges and abundant opportunities inherent to the Great Plains region. The SHP consists of tablelands that occupy approximately 83,000 km^2 of west Texas and eastern New Mexico (Reeves Jr., 1966; Sabin & Holliday, 1995). Bound by the Canadian River to the north and the Pecos River to the south and merging into the Edwards Plateau to the east, the SHP is classified as a semi- arid region, with average annual rainfall ranging from 35.56 cm in western regions to 58.42 cm in the east (Leatherwood, 2010). The SHP serves as an epitome of the short- grass prairie ecosystem that is characteristic of the southern Great Plains (Johnson, 2010; Leatherwood, 2010; Wishart, 2004) (Fig. 1.1).

This area was first documented by the Spanish explorer Francisco Vazquez de Coronado in 1541; however, indigenous peoples had occupied the region for millennia prior to European discovery (Leatherwood, 2010; Wishart, 2004). The SHP was one of the last portions of the United States to be settled (circa 1870s) and developed on a large scale (20th century). With the onset of large-scale irrigation from the underlying Ogallala (High Plains) Aquifer and the discovery of oil and gas reserves, the region was converted into one of the most agriculturally intensive and highest petroleum-producing regions in the United States (Leatherwood, 2010; Smith, Haukos, McMurry, LaGrange, & Willis, 2011; Wishart 2004).

Rapid development and intensive agricultural practices have had significant influences on the ecology of the SHP; these effects are especially highlighted for

the >20,000 wetlands within the region. These wetlands known as "playas" (meaning "beach" in Spanish), are shallow, ephemeral, freshwater wetlands that occur throughout the SHP and are fed via runoff (Bolen, Smith, & Schramm, 1989; Reeves Jr., 1966, Smith, 2003; Sublette and Sublette 1967). Playas of the Great Plains are primarily found from Colorado to Texas (Fig. 1.2), with the highest density of playas in North America occurring within west Texas (Bolen et al., 1989; Smith, 2003; Wishart, 2004). As noted by Smith (2003), playas do occur outside this region (Brough, 1996; LaGrange, 1997; MacKay, Loring, Frost, & Whitford, 1990; Motts, Carpenter, Groat, Matz, & Walker, 1969; Osterkamp & Wood, 1987); however, most scientific studies of playas originate from within the SHP (Smith, 2003).

The term playa (*sensu lato*) has been used to describe a wide variety of geomorphological systems in arid environments that occur in topographically low areas and desiccated former lakebeds (Neal, 1969; Neal, 1975). However, the general use of the term playa incorporates many non-identical landscape features (Neal, 1969; Neal, 1975). This generalized term fails to delineate the diversity of such areas; indeed, playas may contain saline or fresh water, may or may not contain evaporate layers within a basin (e.g. calcium deposits), and experience different hydrology based on drainage and infiltration rates. Playas (*sensu lato*) occur worldwide and are often given regional naming conventions that further complicate comparisons (Neal, 1975; Rosen, 1994), with definitions still in flux (Barth, 2001; Briere, 2000).

Within the SHP, two main categories of playa occur; these include salinas and playas. Salinas are spring-fed discharge basins with high evaporate content (Osterkamp & Wood, 1987) that support regionally rare halophytic communities (Bender, Shelton, Bender, & Kalmbach, 2005). An estimated 40 salinas were present within the SHP; however, many have lost their ground-water connections due to irrigation practices and drought (Rosen, Caskey, Conway, & Haukos, 2013). In contrast, playas are shallow, depressional, recharge wetlands formed from erosion and dissolution processes, each within its own independent watershed (Smith, 2003). As this definition encompasses playas occurring throughout the Great Plains (Smith, 2003), references to playas beyond this point will use this definition (unless explicitly stated otherwise). This definition of a playa is also equivalent to "recharge playa" as found in Rosen (1994).

As the primary regional source of accessible above-ground freshwater, playas of the SHP are critical resources for humans and wildlife, serving as breeding, overwintering, and migration stopover sites for native and migratory taxa (Haukos & Smith, 1994, Smith et al., 2011). Furthermore, the playas of the SHP are part of a continental-scale network of wetlands that facilitates species migration, linking the Southern High Plains ecologically to the rest of the Great Plains (Anderson & Smith, 2004; Baar, Matlack, Johnson, & Barron, 2008; Davis & Smith, 1998; Hall et al., 2004; Ruiz et al., 2014).

Playas also serve as the primary source of recharge for the Ogallala Aquifer, with approximately 95% of all aquifer recharge attributed to infiltration through playa basins (Ashworth, 2006; Ganesan et al., 2016; Nativ & Smith, 1987). Furthermore,

in many urban areas of the SHP, playas are used for stormwater management (Ashworth, 2006; Ganesan et al. 2016; Heintzman, Anderson, Carr & McIntyre, 2015; VanLandeghem, Meyer, Cox, Sharma, Patiño, 2012) and are managed for recreational purposes (Smith, 2003; Young, 2015). Despite their ecological and social importance, however, playas lack legal protection, as they are not subject to Clean Water Act controls, and because most are found on private property, they are highly impacted by human activities (Haukos & Smith, 2003; Mulligan, Barbato, & Seshadri, 2014; Smith, 2003; Tiner, 2003a; Tiner, 2003b).

Playa ecology is governed largely by hydroperiod (the duration of time that a playa is inundated) and thus is highly influenced by surrounding land use (Collins et al., 2014; Smith, 2003; Smith & Haukos, 2002; Tsai, Venne, McMurry, & Smith, 2007). The SHP has been considered the most agriculturally impacted region of North America (Bolen et al., 1989); as such, agricultural land-use/land-cover change and associated effects (e.g. erosion) are considered among the biggest threats to playa functionality (Burris & Skagen, 2013; Daniel, Smith, Haukos, Johnson, & McMurry, 2014; Smith et al., 2011). These studies have highlighted that landscape changes, especially agricultural practices, within the SHP not only influence local ecological processes, but also influence ecological processes at regional and continental scales.

However, landscape change in the SHP is not solely limited to agricultural practices; this region has and continues to experience landscape change as a result of energy extraction expansion and urbanization. However, these two drivers of landscape change are relatively recent and are poorly documented within the SHP

(and especially with respect to playas). Both are projected to increase in scale and economic importance due to ongoing demographic shifts and expanding energy generation capabilities within the SHP, thus magnifying the need for investigations of how these types of landscape changes affect playa system functionality. My research focus therefore will be to investigate the pattern-process relationships associated with energy extraction and urbanization within the SHP, building on a framework of knowledge from studies on how agricultural land use affects playas, and how incorporation of these landscape changes may affect future playa functionality and regional biota.

The first set of objectives (Chapter 2) for my study has been to examine historical and contemporary patterns of energy extraction expansion (specifically oil and natural gas development) within the Texas portion of the playa network, using remotely sensed satellite data and publicly available datasets of known surface well sites for energy extraction. This information was used to quantify how many playas were impacted by surface wells (and their associated pad sites), and relationships with playa size and surface water.

The second set of objectives (Chapter 3) for my study has been to use future climate and growth models, specifically U.S. EPA Integrated Climate and Land-Use Scenarios (ICLUS) A2, A1, and B1 from 2020-2100, to quantify projected rates of impervious surface expansion (as a proxy for urbanization) for playas within the entire Great Plains as a whole, thus allowing for identification of when and where playas are expected to become urbanized (i.e., integrated into urban environments). These findings were compared to those derived independently from USGS FORE-

SCE future climate and growth model projections. Those playas projected to become urbanized by both ICLUS and FORE-SCE can then be prioritized for study or mitigation.

The third set of objectives (Chapter 4) for my study has been to use the USDA National Agriculture Statistical Service (CropScape) land-cover data, USGS Moderate Imaging Spectroradiometer (MODIS) Irrigated Agriculture Dataset for the United States (MIrAD-US) irrigation data, Playa Lakes Joint Venture (PLJV) digital playa wetland database, and species- specific dispersal data in some comprehensive GIS-based landscape connectivity assessments for amphibians. These assessments included Euclidean, least-cost path (LCP), and landscape resistance models (LRM) of amphibian dispersal within the SHP. The connectivity assessments developed in this chapter generated species-specific models of potential dispersal routes for all 13 species of amphibian known to occur with the SHP; these models thus allow for a species-specific determination of available habitats and identification of playas that are critical to maintain regional biotic connectivity in the context of land use/land cover.

My dissertation has generated new knowledge and tested key assumptions of natural and anthropogenic drivers of SHP landscape change. My results have also provided powerful insights on how landscape pattern ultimately impacts playa functionality and biotic processes of playa- dependent wildlife. Additionally, my study has also provided a greater understanding of how landscape change affects the ability of the SHP to function as a conduit of species dispersal.

Lastly, my study may be adapted to mitigate similar challenges faced in other

regions across the Great Plains (e.g. the Prairie Pothole Region, or the Rainwater Basin) and ultimately expanded to other semi-arid regions worldwide experiencing similar challenges (e.g. Caspian Sea region, Canadian prairie provinces, western sub-Saharan Africa).

All chapters of my dissertation have been formatted according to the journal requirements for *Landscape and Urban Planning*. Chapter 3 has already been published in *Landscape and Urban Planning*, https://www.sciencedirect.com/science/article/pii/S0169204619302038.

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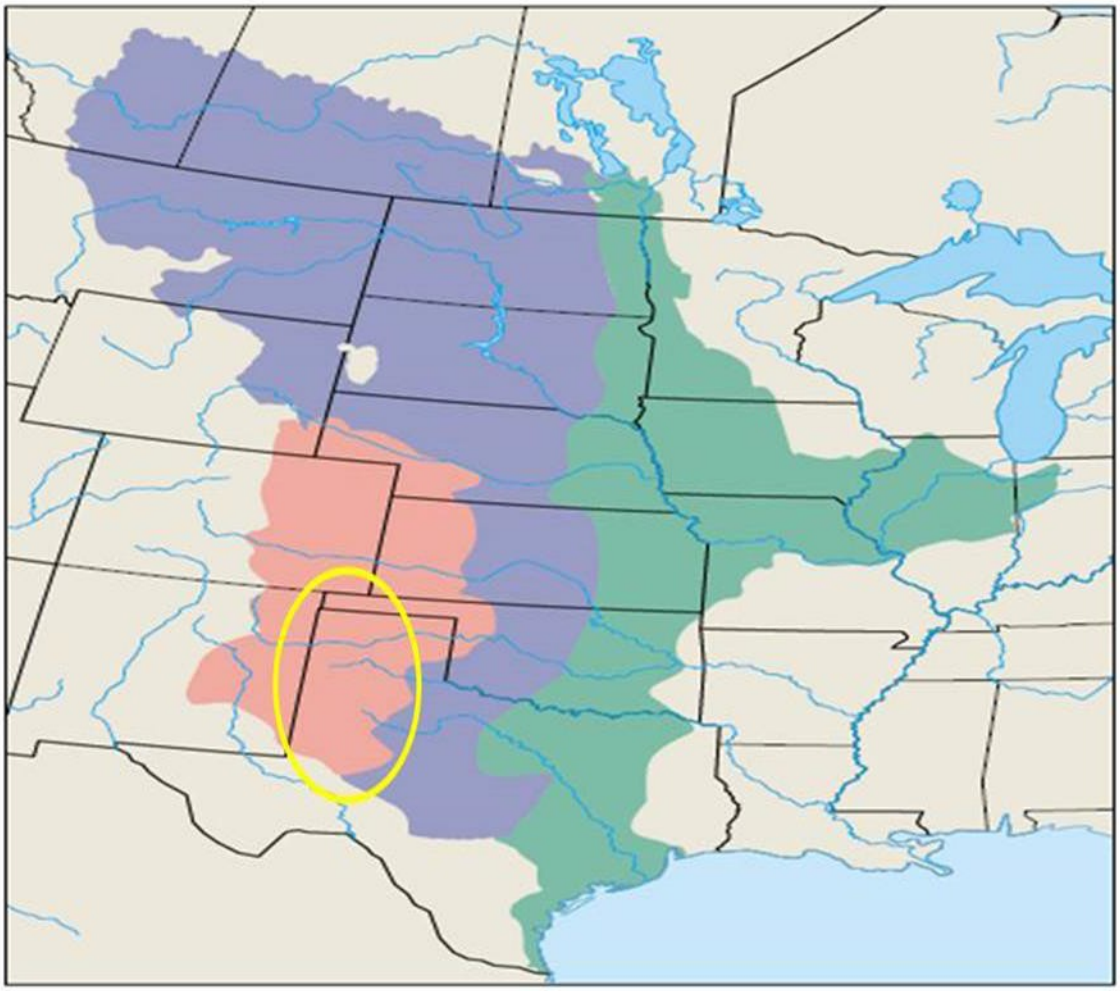

Figure 1.1. Spatial extent of the three main vegetative sub-regions of the Great Plains of North America. Historical distributions of tallgrass prairie are shown in green, mixed-grass prairie in purple, shortgrass prairie in pink, and with the approximate boundary of the Southern High Plains in yellow. Adapted from Mac et al. (1998).

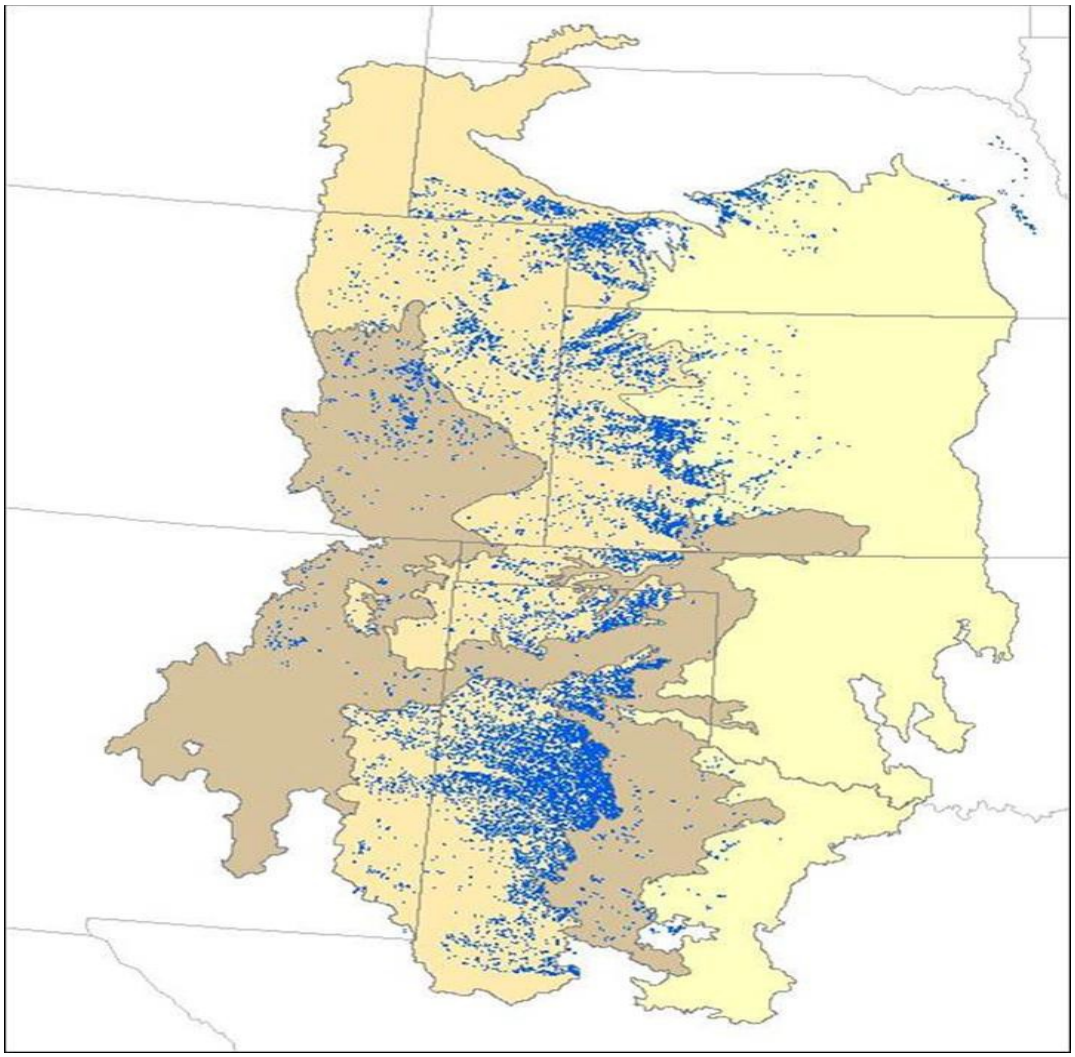

Figure 1.2. Distribution of playas (blue dots) across southern portions of the Great Plains, delimited by U.S. EPA Level III Ecoregions: Southwestern Tablelands (brown), High Plains Ecoregion (orange), and Central Great Plains Ecoregion (yellow). Note the high density of playas in west Texas. Adapted from Playa Lakes Joint Venture's Maps of Probable Playas (http://pljv.org/for-habitat-partners/maps-and-data/maps-of-probable-playas/) and ArcGIS online data.

CHAPTER II

QUANTIFYING PLAYA WETLAND SURFACE-WATER DYNAMICS AS A FUNCTION OF SURROUNDING SURFACE WELL FEATURES IN THE SOUTHERN HIGH PLAINS USING SATELLITE IMAGERY.

Introduction

Energy extraction activities are rapidly expanding worldwide, with unprecedented development of both renewable and non-renewable energy resources that is expected to have considerable ecological impacts (Jones & Pejchar, 2013; Jones, Pejchar, & Kiesecker, 2015; McDonald, Fargione, Kiesecker, Miller, & Powell, 2009). In addition to expansion of renewable energy industries, fossil fuel extraction practices have seen tremendous recent growth that is expected to continue into the near future (Jones & Pejchar, 2013; Jones et al., 2015; McDonald et al., 2009). Within the United States in general and Texas in particular, the expansion of oil and gas extraction are highlighted within the southern Great Plains. Oil and gas production within this region began in the 1920s; since that time, there has been an estimated 29 billion barrels of oil and 2.1 trillion m^3 of gas extracted (Railroad Commission of Texas, 2019a; Railroad Commission of Texas, 2019b). Although energy infrastructure development is not new to this region, it is experiencing recent expansion in terms of the number of new sites (Allred et al., 2015), which is exposing regionally important natural resources to unprecedented forms of anthropogenic activity via direct land conversion for well pads, roads, and ancillary support structures.

For much of Texas, and for the Great Plains as a whole, recent oil and gas development has been driven primarily by hydraulic fracturing ("fracking") (Allred et al., 2015; Lee, 2015; Rahm, 2011). Although the practice of hydraulic fracturing is not new to the oil and gas industry (Gandossi & Von Estorf, 2015) nor to Texas (Railroad Commission of Texas, 2019c), recent expansion of this technology has spurred a national "energy revolution" (Wang, Chen, Jha, & Rogers, 2014) and an energy-development boom in western Texas (Allred et al., 2015; Gallegos, Varela, Haines, & Engle, 2015; Lee, 2015). This surge has exacerbated regional water stress concerns (Freyman, 2014). Oil and gas production, particularly hydraulic fracturing, uses prodigious amounts of water (Gregory, Vidic, & Dzombak, 2011; Vengosh, Jackson, Warner, Darrah, & Kondash, 2014). This is particularly problematic within the southern Great Plains of Texas, where >70% of existing wells occur within areas classified as experiencing extreme water stress, based on numbers of hydraulically fractured wells, groundwater reserves, water resource competition (for agricultural and municipal uses), and drought (Freyman, 2014). Although average water usage per well is considered low by industrial standards (1.1 million gallons per well between 1 January 2011 and 31 May 2013), the region is set to see a doubling of fracturing water use by 2020 (Freyman, 2014). Oil and gas development, including hydraulic fracturing, has been shown to influence turbidity, contamination rates, and hydrology of water resources both in areas situated on and adjacent to extraction sites. Water-quality issues have the potential to extend beyond legal boundaries and may ultimately impact human health (Allred et al., 2015; Entrekin, Evans-White, Johnson, & Hagenbuch, 2011; Gregory et al.,

2011; Karl, 2007; Rahm, 2011; Vengosh et al., 2014). As the southern Great Plains experiences the combined effects of expanding oil and gas development and growing water scarcity concerns, regional aboveground and subsurface freshwater resources are of critical importance.

For the southern Great Plains, focus is on potential environmental impacts to the network of >21,000 shallow, ephemeral wetlands known regionally as playas (Haukos & Smith, 1994; Mulligan, Barbato, & Seshadri, 2014; Smith, 2003). Playas serve as critical habitat for wildlife and, as runoff-fed wetlands, are highly influenced by surrounding land use (Bolen, Smith, & Schramm Jr., 1989; Cariveau, Pavlacky, Bishop, & LaGrange, 2011; Collins et al., 2014; Guthery & Bryant, 1982; Haukos & Smith, 1994; Heintzman, Anderson, Carr, & McIntyre, 2015; Luo, Smith, Allen, & Haukos, 1997; Luo, Smith, Haukos, & Allen, 1999; O'Connell, Johnson, Smith, McMurry, & Haukos, 2012; Smith, Haukos, McMurry, LaGrange, & Willis, 2011; Starr, Heintzman, Mulligan, Barbato, & McIntyre, 2016). Playas are the primary source of recharge of the Ogallala (High Plains) Aquifer (Gurdak & Roe, 2009), which underlies nearly every county in the region and is the main source of freshwater for agricultural irrigation (Guru & Horne, 2000) and oil and gas development in the southern Great Plains (Freyman, 2014).

Development of oil and gas resources has been shown to incur ecological costs (Allred et al., 2015; Brittingham, Maloney, Farag, Harper, & Bowen, 2014; Karl, 2007), and wide-scale expansion of hydraulic fracturing has been particularly controversial (Boudet et al., 2014; North, Stern, Webler, & Field, 2014; Stern,

Webler, & Small, 2014; Wang et al., 2014). However, most previous studies documenting such costs have focused on forested or coastal ecosystems (Baynard, 2011; Baynard, Schupp, Zhang, & Fadil, 2014; Bi, Wang, & Lu, 2011; Dilmore, Sams III, Gloser, Carter, & Bain, 2015; Meng, 2014). The few studies that have occurred within grassland ecosystems have been at small spatial extents (Christie, Jensen, Schmidt, & Boyce, 2015; Nasen, Noble, & Johnstone, 2011), with even fewer examining large-scale oil and gas development in areas dominated by agriculture and private land ownership as in the playa region (but see Allred et al., 2015). Although Allred et al. (2015) examined landscape change, water usage, and primary productivity as a result of energy extraction practices within North America as a whole, discussion of wetlands in that study was limited. Thus, little information exists on the ecological impacts of energy expansions for playas and playa-dependent wildlife, even though playas are critical resources for biodiversity and associated ecosystem services (Haukos & Smith 1994; Gurdak & Roe, 2009; Guru & Horne, 2000; Smith et al., 2011).

This lack of information is partly due to both spatial and legal constraints. Regionally, the vast majority (>90%) of playas occur on private land (Haukos & Smith 1994; Smith et al., 2011).

Furthermore, the abundance and expansive distribution of playas, as well as their intermittent inundation and variable hydroperiod, greatly reduces the feasibility and efficacy of direct, ground-based examinations of playa ecology in real time. Additionally, direct examination of the effects of energy-extraction structures would require extensive legal and human safety clearances. Clearly, an alternative, indirect

approach is required. Although energy development is an important economic driver in the southern Great Plains and oil and gas extraction activities have occurred in this area for decades (Lee, 2015), a detailed analysis of landscape-level impacts of energy extraction practices and effects on playas is warranted to inform ongoing regional landscape planning. Specifically, our objectives were: 1) to map the spatial distributions of playas and surface well features across our focal region, and 2) examination of the surface water dynamics -as we have defined as total wet area and percent basin fill- of playa basins subject to surface wells relative to basins lacking wells. We also 3) quantified differences in surface water dynamics among playas (both impacted by surface wells and those absent wells) based on playa basin size, and 4) to assess the influence of precipitation on playa surface water dynamics across spatial and disturbance scales, we performed a bootstrapping analysis investigating percent basin fill as a function of 3-month accumulated rainfall. Thus, our study serves as the first quantification of contemporary rates and distributions of energy-extraction practices and their potential influences on playas, at both local and regional scales.

Methods

Data

Using a combination of GIS and remote sensing, we examined the 46 Texas counties that contained both playas and surface well features (Fig. 2.1). This focal region was based on the Playas and Wetlands Database (PWD) developed by Mulligan et al. (2014) (http://www.depts.ttu.edu/geospatial/center/pwd/data.html, accessed 5 June 2017). This

database mapped 20,704 playas across ~12.7 million hectares of Texas, Oklahoma, and New Mexico. We focused on the Texas portion as the primary region of oil and gas development, an area of ~11.7 million hectares that contained all the playas in Texas (Table 2.1).

For each of the Texas counties in our study extent, we purchased proprietary surface well data (during November 2016, with 224,043 surface well point features) from the Railroad Commission of Texas (RRC), the Texas state agency tasked with management of fossil fuel extraction. Although several forms of surface well data are curated by the RRC, we chose the "Surface Well Only" data to ensure coverage of all 46 counties given limited available project funding. Our purchased data did not include well installation date, with no guarantee that even higher-priced proprietary data layers would contain that information. Additionally, although surface wells are expected to be provided a unique API (American Petroleum Institute) number, multiple surface well locations within the RRC had the same value or lacked such a number altogether. Lastly, the spatial accuracy of surface well features are not guaranteed by the RRC. However, our November 2016 data represented the best available surface well information available. It also imparted an assumption into our study that all well features were present prior to 1986 (earliest date of Landsat 5 TM satellite imagery). This assumption means that we have likely over-estimated the effect of surface well-induced changes in playa inundation patterns over time. However, given that energy extraction records exist for this region since 1935 (Railroad Commission of Texas, 2019a; Railroad Commission of Texas, 2019b), we feel this assumption is representative of long-term patterns of surface well

development, and germane to the overall ecological context of playas in our focal region and timespan.

Model Development

To assess changes in playa inundation in relation to energy extraction, we adopted an integrated GIS and remote sensing approach with ArcMap 10.6 and ENVI 5.2 software (Collins et al., 2014; Heintzman, Starr, Mulligan, Barbato, & McIntyre, 2017; Ruiz et al., 2014; Starr et al., 2016). We visually inspected all available high-quality (level 9) and cloud-free Landsat images from Landsat 5 TM and Landsat 7 ETM + LT1 from scenes 30/35, 30/36, 30/37, 30/38, 31/35, 31/36, and 31/37 (Fig. 2.1) taken during the peak rainy season (June – September). A total of 49 images from 1986, 1993, 1994, 2001, 2002, 2008, and 2010 (each at 30 m × 30 m resolution) met our criteria and were downloaded from GloVis (https://glovis.usgs.gov/app) (Table 2.2). These images represent the most complete landscape time series for our focal region.

We first spatially projected the PWD and county-scale surface well data to UTM Zone 13 N using the Project Tool in ArcMap 10.6. All county-scale surface well data were then merged into a single layer using the Merge Tool in ArcMap 10.6. We then used ENVI 5.2 to perform Landsat calibration and reflectance calculations for each of our images. These raster layers were subsequently exported as .tif files for analysis. Within ArcMap 10.6, they were projected to UTM Zone 13 N. As final components of initial processing, we clipped away black borders of the imagery using path/row shapefiles (https://www.usgs.gov/land-resources/nli/landsat/landsat-

shapefiles-and-kml-files) and mosaiced each of the 49 Landsat-derived .tif files by scene and year using the minimum operator via the Image Analysis features in ArcMap 10.6.

Because the ecological functionality of playas is driven by dynamic hydrological conditions (i.e., repeated wetting and drying; Haukos & Smith, 2014), we used a band-math classification scheme in ENVI 5.2 to develop binary rasters indicating water and non-water areas within each of our mosaiced .tif layers, following the protocol in Collins et al. (2014). Using the Extract by Mask Tool in ArcMap 10.6, we removed all classified water cells from areas outside of playa basins to eliminate non-playa waters. Fractional rasterization of classified water pixels within or adjacent to playa basins occurred, and some of these cells may have been misidentified due to the minimum raster mosaic processing; we corrected for these issues by excluding those basins that had <10% basin fill from analyses. The Resample Tool was used to covert these now-cleaned layers from 30 m resolution to 3 m resolution, which enabled us to use the Zonal Statistics Tool on the PWD polygon layer to quantify the amount of classified water cells within each playa for each mosaiced yearly dataset via a series of spatial join operators in ArcMap 10.6.

To examine the spatial relationship among playas (either wet or dry) and surface well features, we first used the Buffer Tool in ArcMap 10.6 to create two buffers around each playa feature from the PWD, following the protocols in Collins et al. (2014), Heintzman et al. (2015), and Starr et al. (2016). Our buffers (as "doughnuts") were at 100 m beyond the edge of each playa polygon and at 900 m beyond the first buffer (i.e., 1,000 m radius in total). We then used the Select by

Location Tool in ArcMap 10.6 to identify all playas with surface wells within their basins (i.e., surface well point data intersected playa basin polygon layer) and exported these polygons as a new shapefile. This process was then repeated for both buffered layers to generate shapefiles for the 100 m and 1,000 m scales. We applied the same technique to identify and extract polygon features that neither contained surface well features directly nor within their associated buffers. Lastly, we performed a modified selection to identify and export all playa polygon features that existed within the 1,000 m buffer on an already altered playa yet themselves were only indirectly subject to modifications due to surface wells. Finally, we inverted our selection process to identify and extract surface well features per individual playas (if applicable) as point layers.

From the above methods, we developed four categories of playas based on their spatial relationships with surface wells (Fig. 2.2). The first category, Local Watershed Assessment (LWA), was formed by combining PWD and inundation data for those playas with direct in-basin surface well features and those with surface well features within 100 m of their edge. The second category, Regional Watershed Assessment (RWA), contained those playas with surface well features within 1,000 m. The third category, Indirect Watershed Assessment (IWA), contained those playas that were situated within the 1,000 m buffer of an already altered playa yet themselves were only indirectly subject to modifications due to lack of surface wells present within their own buffer. The fourth category, Non-associated Watershed Assessment (NWA), contained those playas that neither contained surface well features directly nor within their associated buffers.

These four categories served as the foundation for analysis. Given the spatial distribution of surface well features, some playas met the classification requirements for inclusion in both the LWA and the RWA and thus were analyzed as both. As a result, the LWA and RWA are nested and thus not independent. We acknowledge this consideration, yet we feel it prudent to maintain our categorical groupings. This lack of independence is a consequence of real-world patterns, which we feel ought to be preserved in order to effectively represent our focal region and ultimately to direct landscape management practices.

As the PWD natively contained playa basin size information and landscape changes occur among a range of playa basin sizes (Collins et al., 2014; McIntyre, Collins, Heintzman, Starr, & van Gestel, 2018), we examined differences in basin size among each of our categories using ANOVA with Tukey's HSD in VassarStats: Website for Statistical Computation (http://vassarstats.net/). Because playas are runoff-fed, their inundation patterns (and hence their value to wildlife) are the result of how precipitation runoff is affected by surrounding land-use activities (such as energy extraction). Precipitation fluctuates in intensity both spatially and temporally, and measurements of precipitation are constrained by many of the same limitations as when attempting to access playas and surface well locations. We therefore used NOAA National Centers for Environmental Information (NCEI) weather station data from each of the three major regional airports within our focal area (Amarillo International Airport [Amarillo], Lubbock International Airport [Lubbock], and Midland International Airport [Midland]; https://www.ncdc.noaa.gov/cdo-web/datatools/findstation). Using R (R Core Team,

2019), we developed a bootstrapping function with 95% confidence intervals to evaluate the effects of accumulated precipitation summed from a 3-month cumulative widow (prior to the earliest acquisition date from the mosaiced .tif layers) for each playa in each category (LWA, RWA, IWA, and RWA) for each focal year (Collins et al., 2014). We assigned precipitation data from major regional airports to playas using the Near Tool in ArcMap 10.6. Lastly, we also examined differences in percent basin fill among each of our categories using ANOVA with Tukey's HSD in VassarStats. In previous analyses, we considered four categorial groupings (LWA, RWA, IWA, NWA) of playas/surface well relationships. These initial categories were based explicitly on spatial distributions of features, which for the LWA, RWA, and NWA were also justifiable based on the ecological consideration that playa watersheds are independent (Bolen et al., 1989, Haukos & Smith, 1994). However, while the relationships of the IWA are spatially relevant, the IWA definition does not adequately address playa watershed independence (i.e., is an artefactual consequence of our playa/surface well spatial categorical development). From an ecological standpoint, playas of the IWA are most akin to NWA playas. Thus, we merged data from these categories into a single category (IWA+NWA) for sections 3.4 and 3.5.

Based on a lack of *a priori* information on interactions among playa surface water dynamics, precipitation, and energy extraction practices, we followed a first principles approach when developing our predictions among these factors. We first predicted: A) that 3-month accumulated rainfall is positively related to percent basin fill of playa basins regardless of any spatial association with surface wells.

We also predicted: B) that average playa basin size would vary among each of our analysis categories; with the LWA consisting of the smallest playa basins, as they are likely subject to the fewest obstacles to development. Similarly, we also expected smaller playa basins within the RWA relative to the IWA and NWA.

Relatedly, we also predicted: C) that average percent basin fill would vary among each of our analysis categories; with the LWA consisting of lower average percent basin fill than each of the other categories due to direct modifications to a playa basin's ability to retain water (via alteration/destruction of hydric clay soils; Johnson et al., 2012). Furthermore, the RWA ought to then have a lower average percent basin fill compared to the IWA and NWA.

Results

Accounting and Distribution of Spatial Relationships by Category (Table 2.3, Fig. 2.3)

Categorical Summaries

For a comprehensive depiction of all categories simultaneously see Fig. 2.3A, where depiction of individuals categories is as follows. A total of 882 playas had surface well features within their basins (Fig. 2.3B); an additional 2,085 playas had well features within 100 m (Fig. 2.3C). Collectively, these first two groups form the LWA. These playas occurred primarily in northern and southern counties of our focal area, a pattern that reflects the distribution of known regional fossil fuel reserves (Freyman, 2014). At larger scales, 6,316 playas were within 1,000 m of a surface

well, and when playas of the LWA were added, a total of 8,830 playas constituted the RWA (Fig. 2.3D). Playas of the RWA occurred throughout our focal area, primarily near playas of the LWA. Contrasted to the previous categories, the IWA consisted of 1,958 playas that occurred primarily in central counties of the focal area (Fig. 2.3E). For the 9,916 playas of the NWA, a majority also occurred in central counties, albeit at much higher densities. Additionally, this category also featured many playas proximal to the New Mexico border (Fig. 2.3F).

Surface Water Dynamics by Category LWA and RWA (Table 2.4)

For the LWA during our focal time span (Fig. 2.4), 1986 was the wettest year, with the maximum number of inundated playas and a correspondingly minimum number of dry playas. Interestingly, this year featured the lowest mean inundated playa basin size (i.e., a larger proportion of smaller playas were inundated) yet had the highest mean percent basin fill (i.e., those playas that were inundated were "fuller"). However, for dry playas, 1986 featured the lowest mean basin size. This indicated that larger playas were disproportionately inundated. These metrics and the spatial distribution of inundated vs. dry playas indicate that during 1986, playa inundation occurred in a bi-modal fashion, with numerous small and some large playas inundated simultaneously. By 1993, there was a precipitous drop in the numbers of inundated playas, and it featured the minimum mean percent basin fill across our timeframe.

There was a small increase in the number of inundated playas in 1994, yet by 2001 numbers of inundated playas was at a minimum. Indeed, 2001 would be considered the most dry year. By 2002, the numbers of inundated playas were like 1994 levels.

In 2008, the numbers of inundated playas had again dropped, and featured the lowest mean wet area of inundated playas (i.e., lowest levels of surface water in total among playas across the landscape). Also in 2008, dry playas reached their highest mean basin size. Lastly, in 2010, inundated playa numbers slightly increased and occurred with a maximum for mean inundated playa size and highest mean wet area, suggesting that larger playas were filled disproportionately. The spatial distribution of wet and dry playas of the LWA were dynamic across time, with dry playa occurrence more common near the southern edge of our focal extent.

For the RWA during our focal timespan (Fig. 2.5), 1986 again featured the greatest number of inundated playas, with a similar pattern as the LWA for 1986 in terms of mean inundated playa basin size and mean percent basin fill. Likewise, the number of dry playas and their associated mean basin size also featured minimum values. Like the LWA, 1986 would be considered the most wet year for the RWA. There was also a precipitous reduction in the number of inundated playas in 1993; that corresponded with a minimum mean percent basin fill. Furthermore, dry playas reached a maximum value during RWA's most dry year. By 1994 the number of inundated playas had nearly doubled. Yet by 2001, the numbers of inundated playas again dropped. In 2002, a near doubling of inundated playas again occurred. During 2008, however, there was a reduction in the number of inundated playas, and for those playas that did fill, their mean wet area was at a minimum. Also in 2008, the mean basin size of dry playas reached its maximum value. By 2010, there was a small gain in the number of inundated playas, which were on average larger and had more total surface water present; than at any other point during our focal time span. The spatial

distribution of wet and dry playas of the RWA was also dynamic through time, with dry playas tending to occur near the southern border of our extent like the LWA.

Surface Water Dynamics by Category IWA and NWA (Table 2.5)

The IWA had its wettest year in 1986, with the greatest number of inundated playas (Fig. 2.6) and highest mean percent basin fill during our focal time span. Dry playas of the IWA were at a minimum and were comparatively smaller. The IWA had its dry year in 1993 during which the number of inundated playas were at a minimum. Those playas that did hold water were comparatively large but were minimally filled. The number of dry playas was at a maximum in 1993. By 1994, there was modest increase in the number of inundated playas, yet these playas featured the minimum amount of surface water on the landscape for the focal timespan. There was a small drop in the number of inundated playas by 2001; interestingly, however, there was an equal number of inundated playas in 2002. However, since that the mean inundated basin size was the smallest recorded and mean dry playa size was the largest recorded for 2002, these data underscore the fact that surface water dynamics are not simply a function of numbers of inundated playas. By 2008 there was again a minor increase in the number of inundated playas, with a similar trend in 2010. The spatial distribution of wet and dry playas was dynamic through time; however, wet playas more frequently occurred in the central and east-central counties of the focal region.

Like each of the previous categories, the NWA also had its wettest year in 1986 (Fig. 2.7). The number of inundated playas and mean percent basin fill were each at maximum values, whereas the number of dry playas and mean basin size were each

at minimum values. Following the patterns shown in the other categories, 1993 featured the lowest number of inundated playas, and those that did fill were on average larger. As expected, the number of dry playas was highest during this year. By 1994, there was a modest increase in the number of inundated playas, with larger gains in 2001. In 2002, however, there was a relatively sharp decrease in the number of inundated playas, and those did hold water were on average smaller. Another minor increase in the number of inundated playas occurred in 2008; however, mean wet area and mean percent basin fill were both at minimum values, indicating playas only marginally filled and correspondingly limited amounts of surface water on the landscape. Although not the driest year, mean dry basin size was at a maximum. Lastly, in 2010, there was a moderate increase in the numbers of inundated playas. The spatial distribution of NWA playas was again dynamic, and from 2001 onward most inundated playas occurred in central or east-central counties.

Assessment of Precipitation on Playa Inundation by Category

Results indicated that playa inundation patterns across our categories and focal timespan was dynamic. However, given the static nature of imagery, this type of analysis was incapable of assessing the influence of precipitation and associated runoff on the occurrence of inundated playas.

We first plotted our percent basin fill results as a function of 3-month accumulated precipitation from each our NCEI locations across all focal years (Fig. 2.8). The plot, which consists of yearly colored dots, represents an individual playa's percent basin fill along the axis of accumulated 3-month precipitation for a given year. The plot supports our previous observations that 1986 was indeed the overall most wet

year across all categories at each location, based on the number of inundated playas and precipitation amounts. However, there were differences in what would be considered the driest year at individual NCEI scales. This is most easily recognized for the year 1993, where playas associated with the Amarillo NCEI featured relatively high precipitation rates, with drier conditions around the Lubbock NCEI. Fig. 2.8 also helps to partially explain the previously described north-south gradient in observed inundated playas in Figures 2.4-2.7, as climatically the northern portions of Texas typically receive greater annual precipitation. Additionally, the plot highlights the differences among the spatial distribution of playas themselves, indicated by how solid the lines of dots are within in each sub-plot. The Lubbock NCEI area included the most playas, and the Midland NCEI had the fewest (Amarillo NCEI had an intermediate number of playas). The Amarillo NCEI had most of its playas categorized as RWA or NWA, with fewer in the LWA and IWA. In contrast, playas near Midland NCEI were mostly LWA and RWA, with very few IWA or NWA. Playas near Lubbock NCEI were more evenly distributed among categories. These patterns align themselves with the distribution of surface wells as shown in Figure 2.1.

When examining the effects of average percent basin fill as a function of 3-month accumulated precipitation (Fig. 2.9), there were positive, negative, and non-significant relationships. Each individually colored dot represents the average percent basin fill for all playas for a given year among each possible combination of analysis category and NCEI location. The blue line represents a linear regression applied to the trends in each sub-plot, with ranges of sensitivity in gray. The

Amarillo NCEI sub-plots indicated that for the LWA, presence of surface wells was slightly negatively correlated with average percent basin fill. At the RWA scale, the relationship was non-significant. However, a moderately positive relationship was observed for the IWA, with a slightly positive relationship also observed for the NWA. The Lubbock NCEI sub-plots indicated slightly positive relationships across each analysis category. The relationship that occurred within the Midland NCEI for the LWA was non-significant, whereas that of the RWA were slightly positive. A non-significant relationship occurred with the IWA, and a moderately negative relationship existed for the NWA.

Assessment of Basin Size by Category

ANOVA and Tukey's HSD tests (Supplementary Material) indicated that there were significant differences in playa basin sizes among the LWA, RWA, and IWA+RWA. However, contrary to our initial prediction, playa basins of the LWA were on average larger (9.10 ha) than those in either the RWA or the IWA+RWA. Playa basins of the RWA were on average the smallest (6.87 ha), with those of the IWA+RWA intermediate (8.15 ha) among categories.

Assessment of Percent Basin Fill by Year per Category

The relationships among average percent basin fill and analysis category were variable through time (Supplementary Material). During 1986, ANOVA indicated a marginally significant difference ($p = 0.04$) in average percent basin fill among categories; however, Tukey's HSD post-hoc tests indicated that no significant differences among pairs of categories existed. By 1993, all relationships were non-significant ($p = 0.36$). In 1994, however, both the ANOVA ($p < 0.01$) and Tukey's

HSD ($p < 0.05$) indicated significant differences in average percent basin fill between the RWA and the IWA+NWA. In this case, the RWA had a higher average percent basin fill (51%) compared to the IWA+NWA (46%), which was counter to our initial prediction.

By 2001, all relationships were again non-significant ($p = 0.09$). During 2002, both ANOVA ($p < 0.01$) and Tukey's HSD ($p < 0.05$) indicated a significant difference between the RWA and the IWA+NWA. Again, contrary to our original prediction, the RWA consisted of higher average percent basin fill (57%) than the IWA+NWA (52%). For 2008, ANOVA indicated a significant difference among categories ($p < 0.01$), and Tukey's HSD revealed that the LWA ($p < 0.05$) and the RWA ($p < 0.05$) both had higher average percent basin fill (46% and 47%, respectively) than the IWA+RWA (43%). Finally, in 2010, ANOVA ($p < 0.01$) and Tukey's HSD ($p < 0.05$) indicated that a new pattern had emerged, where the IWA+NWA had larger average percent basin fill (58%) than the LWA (53%). Only this relationship matched our prediction. In total there were four instances of relationships not matching our predictions.

Discussion

Our results indicated that playa inundation patterns (and, by extension, playa functionality) were dynamic in space and time. This phenomenon has been previously documented with respect to playas and often attributed to agricultural and municipal land-use/land-cover changes, variable precipitation patterns, and the interaction between these two factors (Bolen et al., 1989; Collins et al., 2014; Haukos

& Smith, 1994; McIntyre et al., 2018; Ruiz et al., 2014). Our study is the first to ascribe part of this dynamism to number and proximity of oil and gas wells. Although the existence of some playa-surface well relationships (Johnson, Haukos, Smith, & McMurry, 2012; Mulligan et al., 2014) have been documented previously, our study represents the first to quantitatively link each of these factors across multiple landscape scales (100 m and 1,000 m) through time. Furthermore, our study is also the first of its kind to document playa-surface well relationships among inundated and dry playas across time. Dry playas should not be discounted, especially given that the role that playas fill in supporting regional biodiversity is dependent upon cyclic inundation and drying events (Haukos & Smith, 1994).

Specifically, as shown by our bootstrapping analysis in Fig. 2.9, patterns of inundation were dynamic among categories and NCEI locations, which consisted of positive, negative, and non- significant relationships. The mixed nature of these results may be due in part to data limitations encountered in our time-series analysis. For example, our surface well data layers did not contain data on installation date. This imparted an assumption that all surface well locations had existed since 1986, which is highly improbable. This assumption potentially inflated the numbers of playas across each of our analysis categories. Furthermore, we used precipitation data from regional airports because they had the most complete temporal records; however, the values derived from these locations may be poor proxies to conditions found in situ. Use of these proxy values had the potential to both underestimate and overestimate the effects of precipitation.

Furthermore, we acknowledge that these data limitations could alter the slopes

our best-fit trendlines, as theoretically the trendline could "wobble" within the entirety of its associated sensitivity ranges. Despite these limitations, common to other time-series analyses of playas (Collins et al., 2014; McIntyre et al., 2018, Ruiz et al., 2014), our study provides a means to appraise playa-surface well relationships without logistical or legal constraints, making our results pertinent and germane for regional landscape planning purposes.

Indeed, from the perspective of landscape planning, our results may be especially intriguing. It appears that for some localities, the presence of surface wells is positively associated with playa inundation and increased average percent basin fill, possibly because well pads and ancillary infrastructure (e.g. access roads) may facilitate runoff. However, we caution against any attempt to justify unrestrained development near playas in a purported effort to increase the occurrence of water within playa basins. The influence of this potential scenario on water quality remains unknown but is feasibly detrimental. Relatedly, given the mechanical requirements of hydraulic fracturing, the positive relationship between surface wells and playas may in part be a consequence of the use of playas as natural "fracking ponds" (treatment and storage locations of water post-extraction) (Vengosh et al., 2014). As an additional intriguing landscape planning consideration, our study also provided the first quantitative evidence of a positive link between increasing playa basin size and severity of surface well impacts. Currently, we are unable to provide a causative agent for this relationship. However, perhaps larger basins are more likely be impacted by surface wells strictly from an area perspective (i.e., larger basin equates to a larger target). Alternatively, if larger playas just happen to occur more often in

regions of underground extractable fossil fuel reserves, then a "just so" answer could explain this pattern. Admittedly, each of these speculative causative agents are not likely scientifically appealing; as such, we would encourage further investigations into this positive linkage. For those localities that had negative inundation relationship patterns between playas and surface wells, it is possible that the development of wells may deteriorate the characteristic clay soils of playa basins. When these clay soils are disturbed, the ability of a playa to retain water is diminished (Johnson et al., 2012).

Regardless of relationship direction (positive, negative, or non-significant), the possibility exists that other factors outside the scope of this study (e.g. irrigation practices) may be masking relationships between playas and surface oil and gas wells. Indeed, the relationships documented in our study represent a snapshot of ecological conditions. Thus, the relationships among playas and surface wells themselves may be transitory due to changes in development patterns and individual stakeholder actions. Relatedly, we caution against simply describing playa hydrology as a function of regionally wet years vs. dry years, as local patterns of precipitation and land-use/land-cover changes act in tandem to determine whether a given playa basin can and does hold water at any given time.

Conclusions

Our study documented a diverse array of relationships among land-use/land-cover change (in the form of surface wells), basin size, and precipitation that influence playa inundation. Although our analyses were constrained by data

limitations, such limitations are present in nearly all time-series analysis. Our study also represents an economically inexpensive and ecologically unobtrusive means of investigating land-use/land-cover change that can be adapted for other areas where wetlands are subject to increasing energy extraction practices.

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Table 2.1. List of focal Texas counties with playas and surface well features analyzed.

Andrews	Castro	Dickens	Glasscock	Hockley	Lynn	Oldham
Armstrong	Cochran	Donley	Gray	Howard	Martin	Parmer
Bailey	Crosby	Ector	Hale	Hutchinson	Midland	Potter
Borden	Dallam	Floyd	Hansford	Lamb	Moore	Randall
Briscoe	Dawson	Gaines	Hartley	Lipscomb	Motley	Roberts
Carson	Deaf Smith	Garza	Hemphill	Lubbock	Ochiltree	Sherman

Table 2.2. Scene list and dates (month/day/year) of Landsat imagery analyzed in our study. White cells indicate Landsat 5 TM imagery and gray cells indicate Landsat 7 ETM+LT1 imagery.

Scene 31/35	**Scene 31/36**	**Scene 31/37**	**Scene 30/35**	**Scene 30/36**	**Scene 30/37**	**Scene 30/38**
9/18/1986	9/18/1986	9/18/1986	9/11/1986	9/11/1986	9/11/1986	9/11/1986
9/21/1993	9/21/1993	9/21/1993	9/30/1993	9/30/1993	9/30/1993	9/30/1993
9/24/1994	9/24/1994	9/24/1994	9/17/1994	9/17/1994	9/17/1994	9/17/1994
6/15/2001	6/15/2001	6/15/2001	6/24/2001	6/24/2001	6/24/2001	7/10/2001
6/10/2002	6/10/2002	6/10/2002	6/19/2002	6/19/2002	6/19/2002	6/19/2002
6/10/2008	6/10/2008	6/10/2008	6/3/2008	6/3/2008	6/3/2008	6/3/2008
9/4/2010	9/4/2010	9/4/2010	9/29/2010	9/29/2010	9/29/2010	9/29/2010

Table 2.3. Accounting of spatial relationships by category. NA = not applicable.

Analysis of Spatial Relationships by Category		**# of Playa Basins**		**# of Surface Wells**
Total number of playa basins analyzed from PWD		**20,704**		
Total number of surface well features analyzed from RRC				**224,043**
Playa basins with surface well features directly within basins		882		1,075
Playa basins with surface well features within 100 m	+	2,085	+	3,099
A total of 393 playas basins met both categorical definitions and were removed to avoid duplication	-	*393*		
These groupings constituted the LWA	=	**2,514**	=	**4,174**
Playa basins with surface well features within 1,000 m		6,316		51,042
When playa basins and surface well features of the LWA that also meet this categorical definition are included	+	*2,514*	+	*4,174*
These groupings constituted the RWA	=	**8,830**	=	**55,216**
Playa basins indirectly affected by surface well features which constituted the IWA	=	**1,958**		NA
Playa basins with no surface well features within their basins or buffers constituted the NWA	=	**9,916**		NA
Surface well features not associated with playa basins		NA	=	**164,653**

Table 2.4. Metrics of surface water dynamics of playas in the Local Watershed Assesment and Regional Watershed Assessment by year. Values in bold represent maximum metric values by category, whereas italics indicate minimum metric values by category. Gray shading indicates results for dry playas only.

Category	Year	# of Inundated Playas	Mean Inundated Playa Basin Sizes (ha) (range)	Mean Wet Area of Inundated Playas (ha) (range)	Mean Inundated Playas % Basin Fill (range)	# of Dry Playas	Mean Dry Playa Basin Sizes (ha) (range)
LWA	1986	**1,124**	*12.15 (0.09 - 341.39)*	5.14 (0.01 - 126.64)	**49.34 (<0.00 - >100.00)**	*1,390*	*6.62 (0.07 - 237.77)*
LWA	1993	191	20.42 (0.32 - 282.37)	4.51 (<0.00 - 70.28)	*30.16 (<0.00 - >100.00)*	2,323	8.16 (0.07 - 341.39)
LWA	1994	318	16.13 (0.18 - 282.37)	4.26 (0.01 - 69.61)	36.03 (<0.00 - >100.00)	2,196	8.08 (0.07 - 341.39)
LWA	2001	*144*	24.25 (0.82 - 282.37)	6.06 (0.04 - 115.17)	34.00 (<0.00 - >100.00)	**2,370**	8.17 (0.07 - 341.39)
LWA	2002	357	15.47 (0.16 - 341.39)	5.96 (<0.00 - 180.73)	42.38 (<0.00 - >100.00)	2,157	8.04 (0.07 - 237.77)
LWA	2008	232	12.98 (0.74 - 282.37)	*3.75 (0.01 - 74.01)*	36.44 (<0.00 - >100.00)	2,282	**8.70 (0.07 - 341.39)**
LWA	2010	258	**25.72 (0.41 - 341.39)**	**11.78 (0.04 - 218.79)**	37.87 (<0.00 - 99.99)	2,256	7.19 (0.07 - 261.04)
RWA	1986	**3,688**	*9.55 (0.07 - 371.13)*	4.52 (<0.00 - 126.64)	**50.89 (<0.00 - >100.00)**	*5,142*	*4.96 (0.04 - 237.77)*
RWA	1993	*593*	14.94 (0.32 - 371.13)	3.65 (<0.00 - 70.28)	*30.81 (<0.00 - >100.00)*	**8,237**	6.29 (0.04 - 341.39)
RWA	1994	1,181	10.26 (0.19 - 282.37)	3.00 (<0.00 - 109.83)	38.60 (<0.00 - >100.00)	7,649	6.35 (0.04 - 371.13)
RWA	2001	794	13.35 (0.25 - 282.37)	3.97 (<0.00 - 115.17)	37.22 (<0.00 - >100.00)	8,036	6.23 (0.04 - 371.13)
RWA	2002	1,365	9.62 (0.16 - 341.39)	3.75 (<0.00 - 180.73)	46.13 (<0.00 - >100.00)	7,465	6.37 (0.04 - 371.13)
RWA	2008	897	9.63 (0.07 - 282.37)	*2.83 (0.01 - 85.94)*	36.06 (<0.00 - >100.00)	7,933	**6.56 (0.04 - 371.13)**
RWA	2010	1,020	**15.36 (0.07 - 341.39)**	**6.85 (0.01 - 218.79)**	40.01 (<0.00 - >100.00)	7,810	5.76 (0.04 - 371.13)

Table 2.5. Metrics of surface water dynamics of playas in the Indirect Watershed Assessment and Non-associated Watershed Assessment by year. Values in bold represent maximum metric values by category, whereas italics indicate minimum metric values by category. Gray shading indicates results for dry playas only.

Category	Year	# of Inundated Playas	Mean Inundated Playa Basin Sizes (ha) (range)	Mean Wet Area of Inundated Playas (ha) (range)	Mean Inundated Playas % Basin Fill (range)	# of Dry Playas	Mean Dry Playa Basin Sizes (ha) (range)
IWA	1986	**901**	8.35 (0.16 - 127.49)	4.48 (0.01 - 40.21)	**50.31 (<0.00 - >100.00)**	*1,057*	*3.87 (0.03 - 71.54)*
IWA	1993	*79*	**12.63 (0.19 - 49.83)**	4.66 (0.05 - 40.35)	*28.77 (<0.00 - 97.80)*	**1,879**	5.65 (0.03 - 127.49)
IWA	1994	253	7.87 (0.19 - 45.10)	*2.44 (0.01 - 31.87)*	35.14 (<0.00 - >100.00)	1,705	5.64 (0.03 - 127.49)
IWA	2001	235	10.84 (0.37 - 60.28)	4.05 (0.04 - 38.40)	35.61 (<0.00 - 99.91)	1,723	5.26 (0.03 - 127. 49)
IWA	2002	235	*7.56 (0.13 - 50.20)*	2.99 (0.01 - 28.80)	42.24 (<0.00 - >100.00)	1,723	**5.71 (0.03 - 127. 49)**
IWA	2008	241	9.36 (0.40 - 42.50)	2.56 (<0.00 - 28.77)	31.30 (<0.00 - >100.00)	1,717	5.45 (0.03 - 127.49)
IWA	2010	286	11.70 (0.56 - 50.20)	**5.90 (0.01 - 47.20)**	45.18 (<0.00 - >100.00)	1,672	4.94 (0.03 - 127.49)
NWA	1986	**5,066**	11.40 (0.04 - 164.43)	5.67 (<0.00 - 138.58)	**49.77 (<0.00 - >100.00)**	*4,850*	*5.65 (0.04 - 165.80)*
NWA	1993	*876*	**16.25 (0.17 - 165.80)**	5.05 (0.01 - 135.34)	31.17 (<0.00 - >100.00)	**9,040**	7.84 (0.04 - 141.10)
NWA	1994	1,025	12.71 (0.24 - 164.43)	3.02 (0.01 - 135.94)	28.58 (<0.00 - >100.00)	8,891	8.11 (0.04 - 165.80)
NWA	2001	1,797	13.93 (0.04 - 164.43)	5.08 (<0.00 - 162.46)	37.16 (<0.00 - >100.00)	8,119	7.40 (0.04 - 165.80)
NWA	2002	926	*11.28 (0.20 - 164.43)*	3.11 (<0.00 - 128.41)	34.55 (<0.00 - >100.00)	8,990	8.31 (0.04 - 165.80)
NWA	2008	996	12.27 (0.17 - 164.43)	*3.01 (<0.00 - 158.00)*	*27.36 (<0.00 - 99.97)*	8,920	**8.18 (0.04 - 165.80)**
NWA	2010	1,464	15.75 (0.08 - 165.80)	**7.22 (<0.00 - 164.10)**	43.48 (<0.00 - >100.00)	8,452	7.35 (0.04 - 141.10)

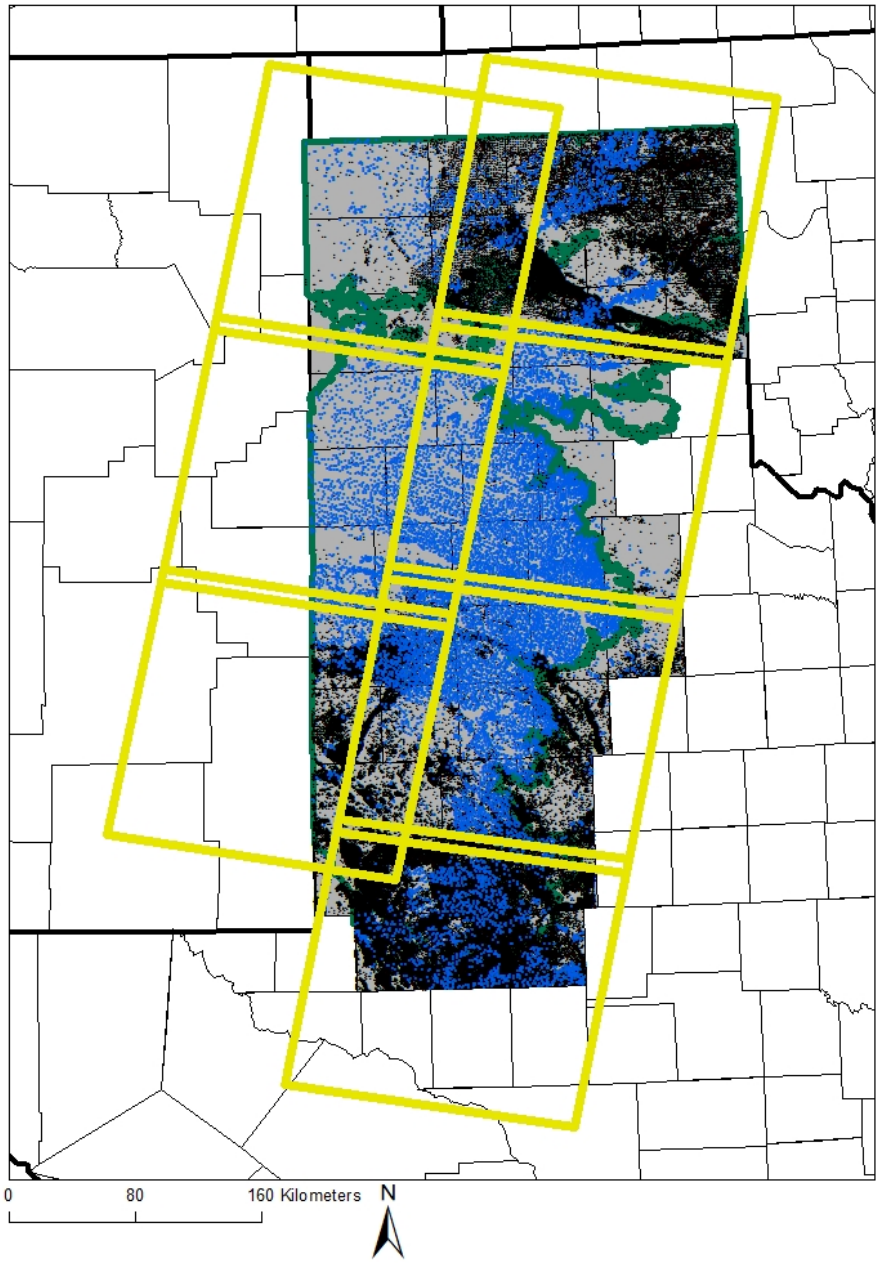

Figure 2.1. Spatial distribution of playas (blue dots) and surface wells (black dots) within focal Texas counties of the PWD (gray polygons). Included is an outline of the Texas portion of the Ogallala Aquifer (dark green) and outlines of the Landsat scenes (yellow parallelograms) used in analysis.

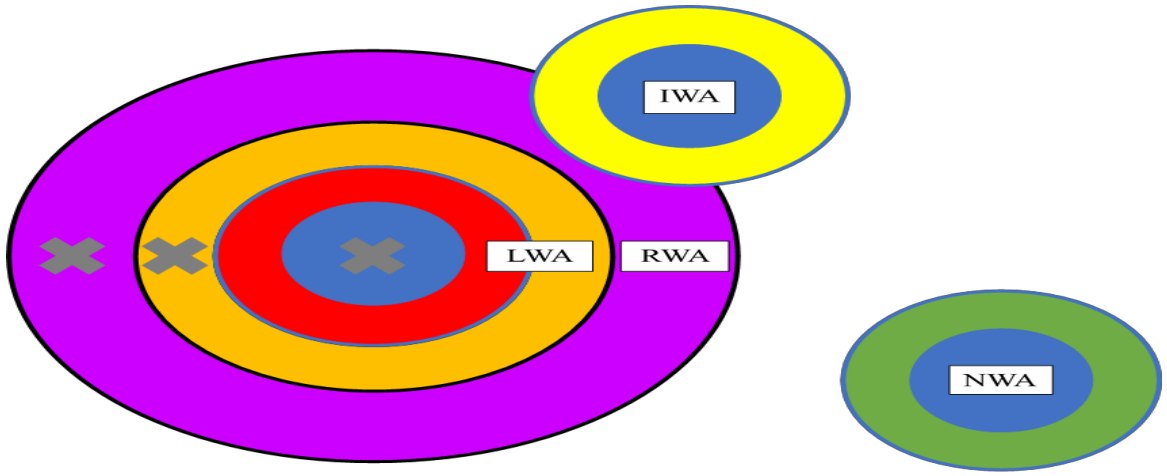

Figure 2.2. Schematic representation of the classification scheme used to assign playas into four analysis categories. Playa basins (blue circles, with blue indicating wet areas within basins and red indicating dry areas of basins not completely full) may have surface wells (gray Xs) directly within their basin and/or within 100 m of their basin edge (orange ring with black outlines). Such playas were classified as Local Watershed Assessment. If a playa had a surface well within 1,000 m of its basin edge (purple ring with black outlines), is was classified as Regional Watershed Assessment. A playa could be both Local Watershed Assessment and Regional Watershed Assessment simultaneously. If a playa occurred within the 1,000 m buffer of an affected playa yet itself was unaffected by surface well features within its own buffers, it was classified as Indirect Watershed Assessment (yellow circle). Lastly, a playa that neither contained surface well features directly nor within their associated buffers was classified as Non-associated Watershed Assessment (green circle).

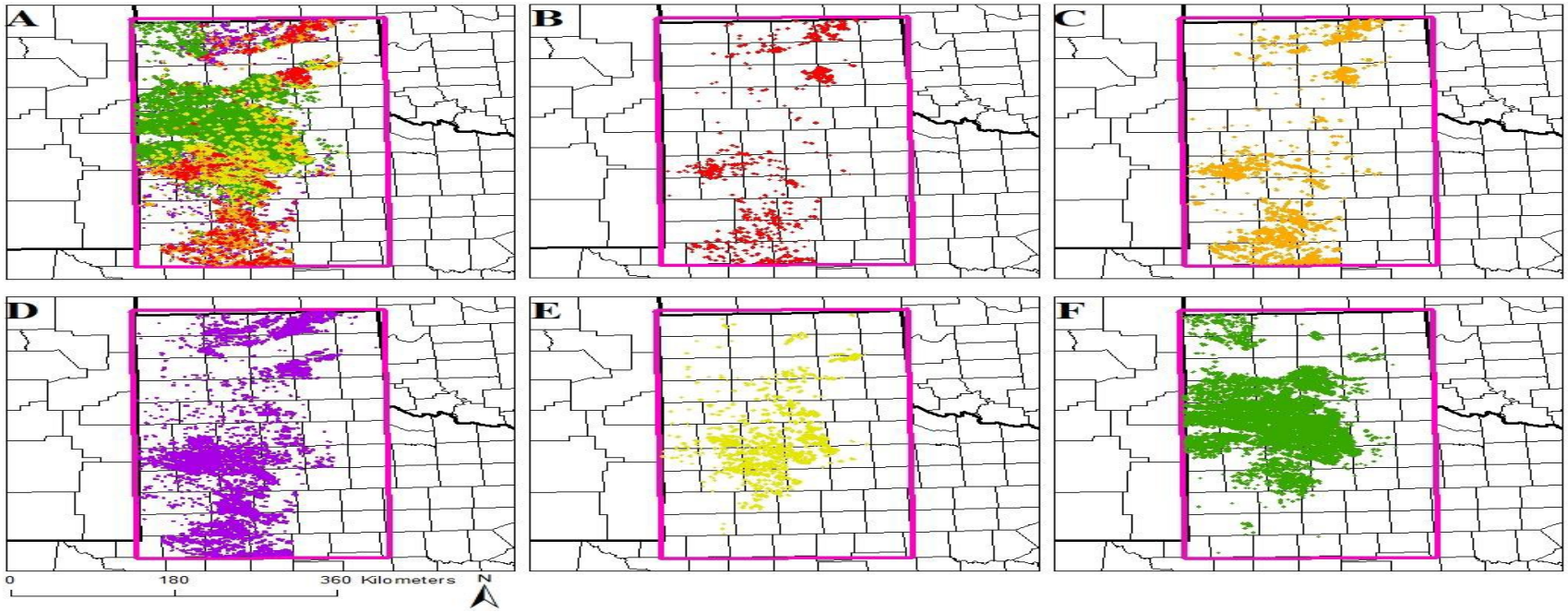

Figure 2.3. Distributions of spatial relationships by category. A) A depiction of all categories simultaneously; because polygon features overlapped, all colors are present but not visible. B) Playas with surface wells within their basin (red polygons) and C) playas subject to surface wells within 100 m of their edge (orange polygons) collectively are Local Watershed Assessment. D) Playas within 1,000 m of surface wells (purple polygons) are Regional Watershed Assessment. E) Playas that were only indirectly subject to surface wells are Indirect Watershed Assessment (yellow polygons). F) Those playas with no wells within 1,000 m are Non-associated Watershed Assessment (green polygons).

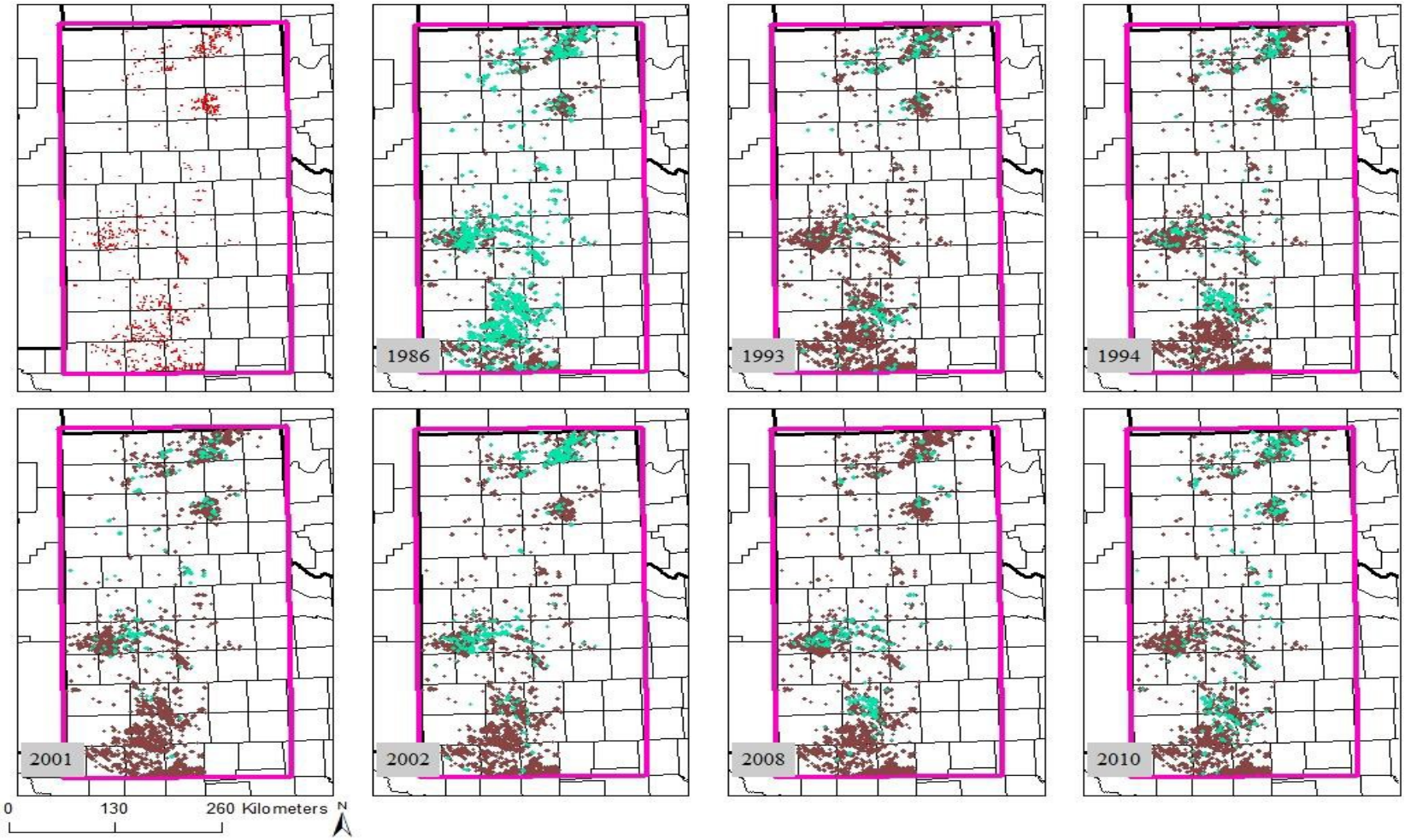

Figure 2.4. Timeline of surface water dynamics of the Local Watershed Assessment with inundated playas (turquoise) and dry playas (brown). For reference, all Local Watershed Assessment playas are depicted in red.

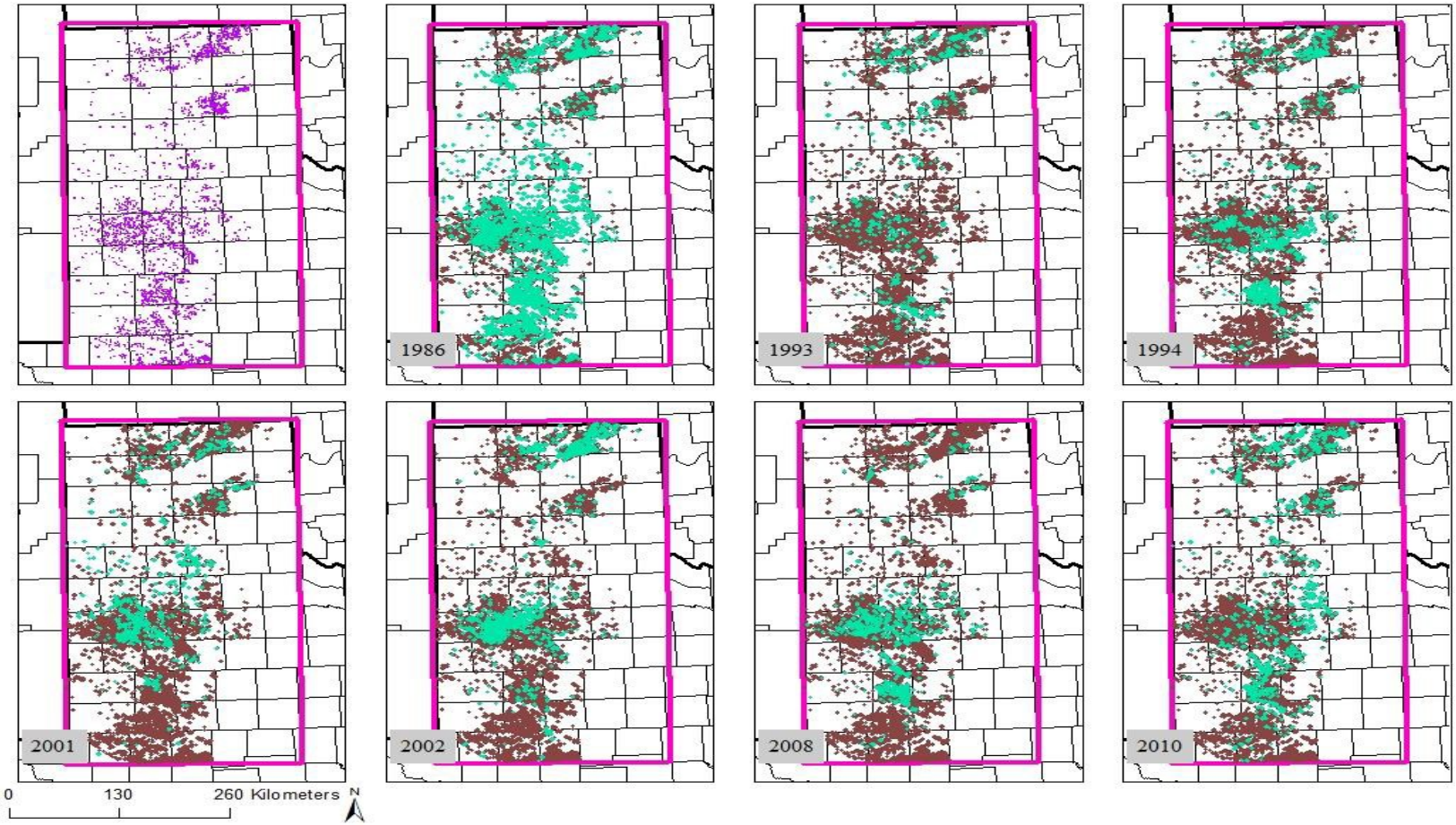

Figure 2.5. Timeline of surface water dynamics of the Regional Watershed Assessment with inundated playas (turquoise) and dry playas (brown). For reference, the Regional Watershed Assessment playas are depicted in purple.

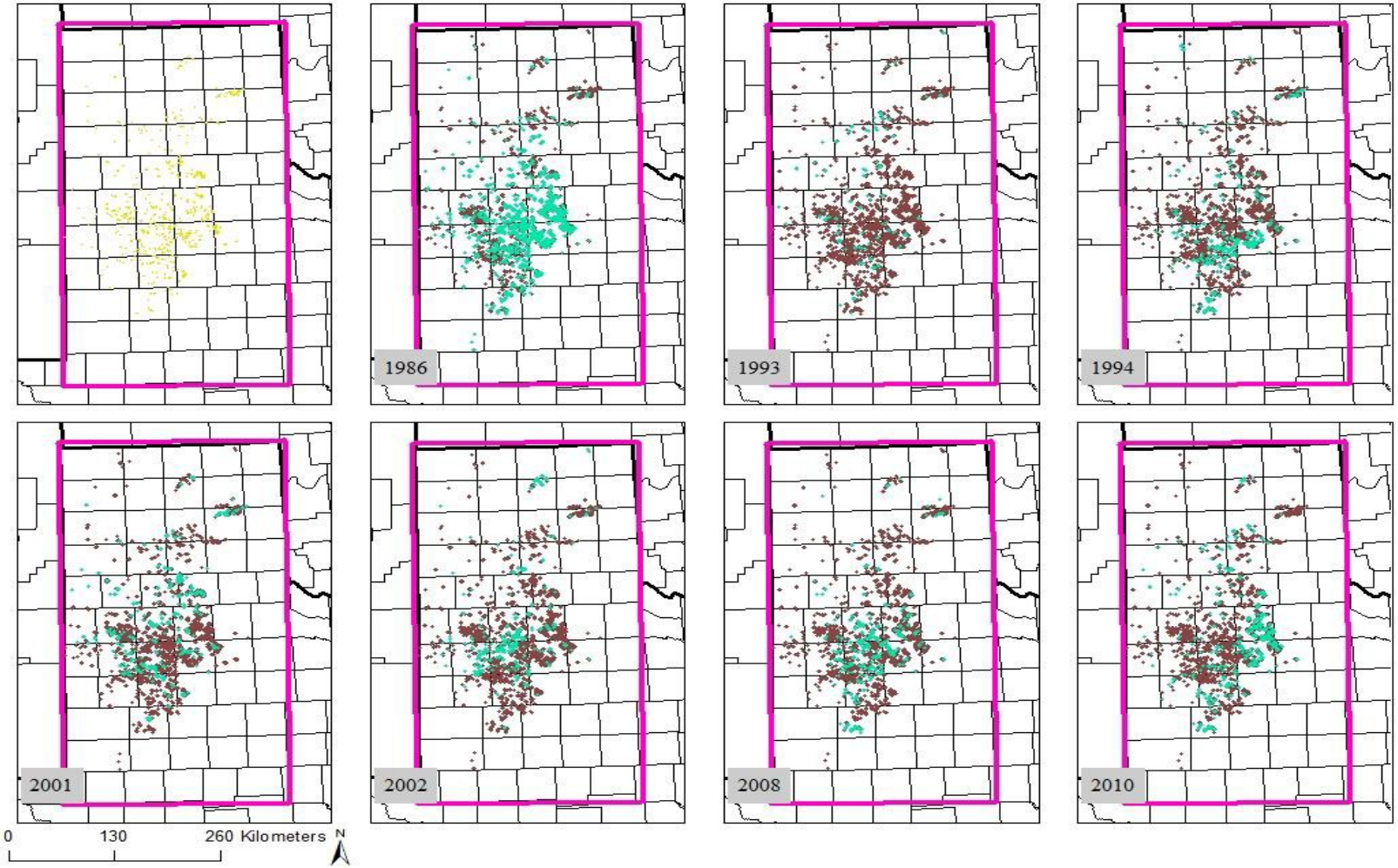

Figure 2.6. Timeline of surface water dynamics of the Indirect Watershed Assessment with inundated playas (turquoise) and dry playas (brown). For reference, the Indirect Watershed Assessment playas are depicted in yellow.

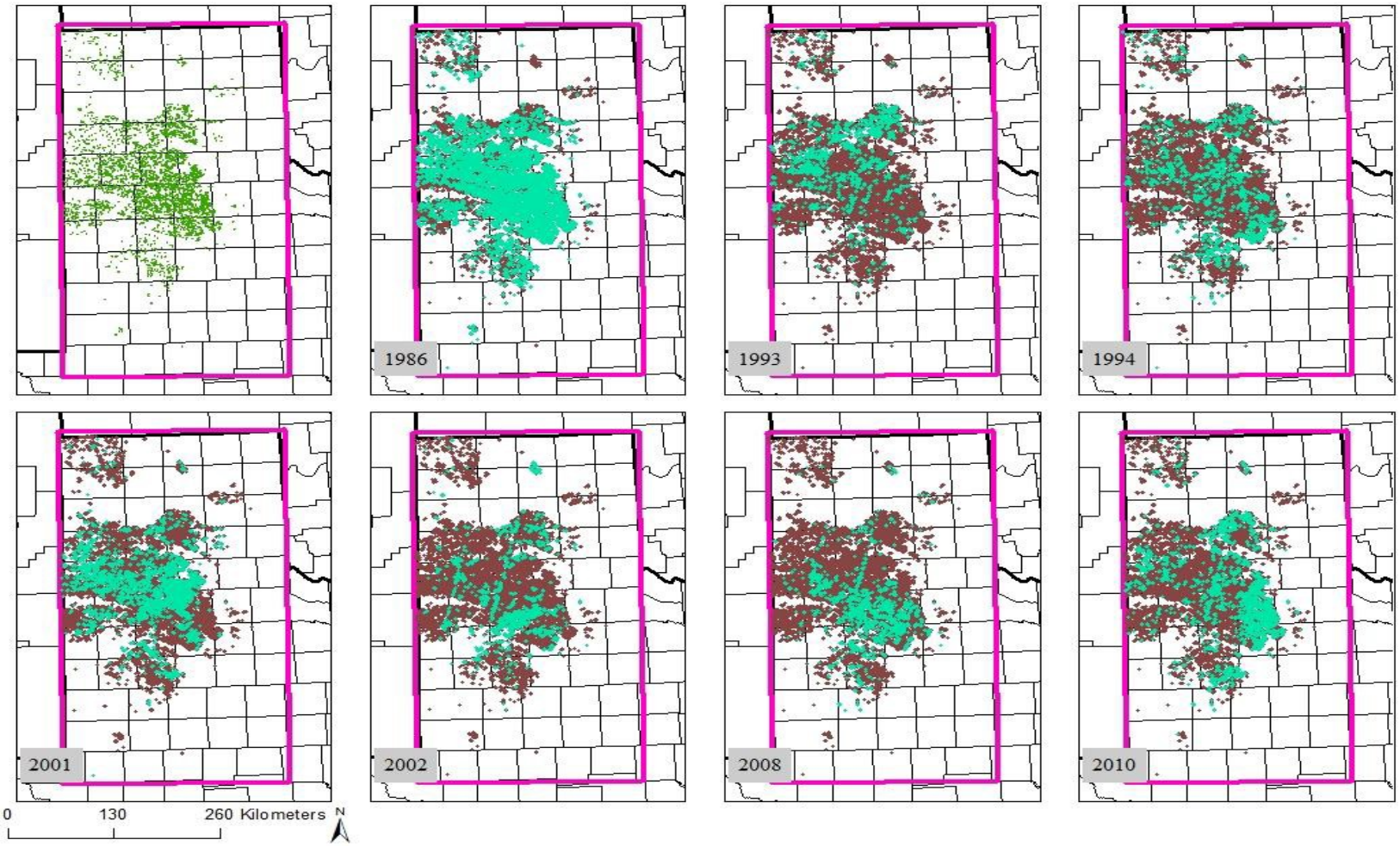

Figure 2.7. Timeline of surface water dynamics of the Non-associated Watershed Assessment with inundated playas (turquoise) and dry playas (brown). For reference, the Non-associated Watershed Assessment playas are depicted in green.

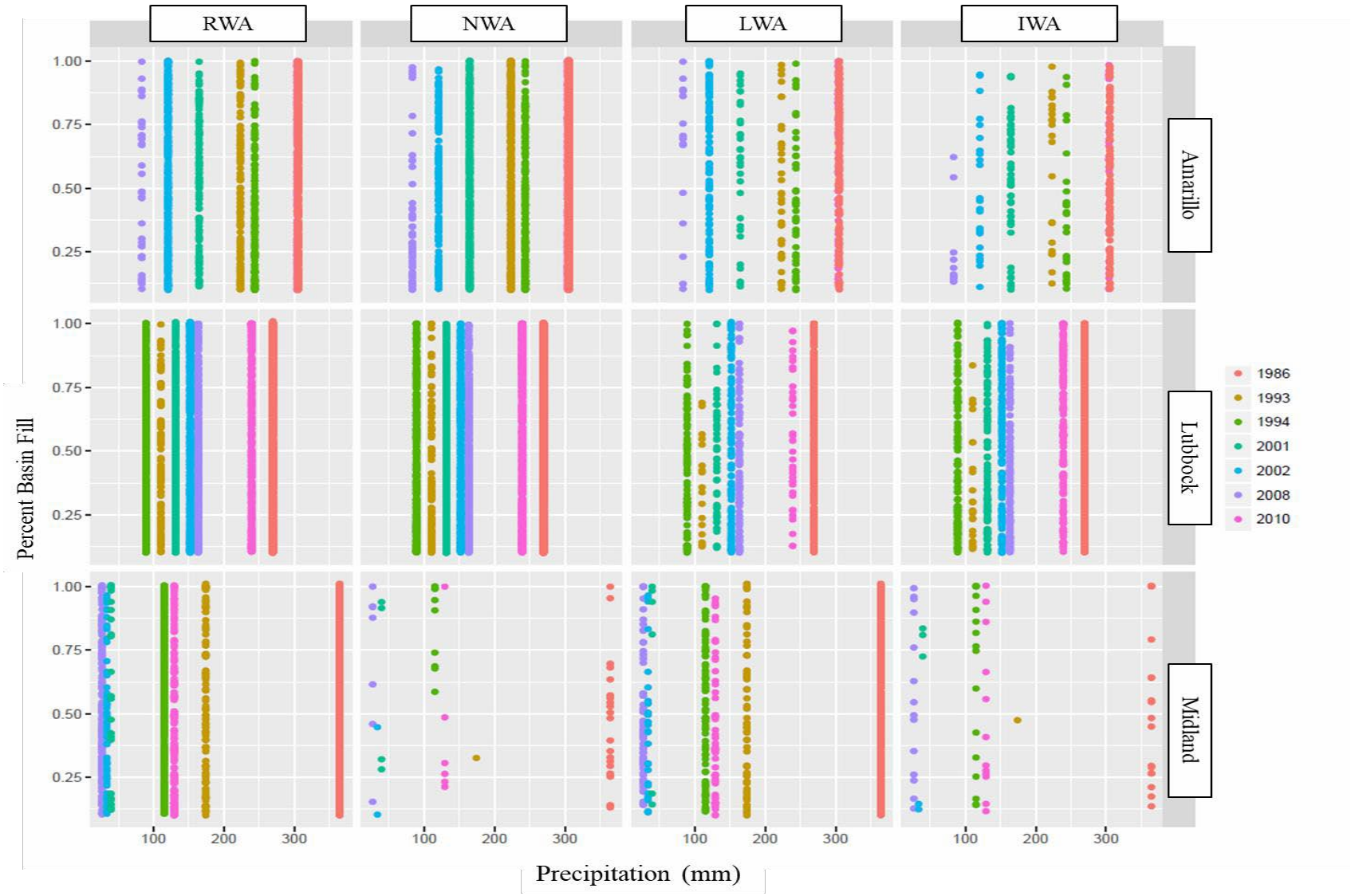

Figure 2.8. Plot of percent basin fill as a function of 3-month accumulated precipitation across categories and NOAA National Centers for Environmental Information locations.

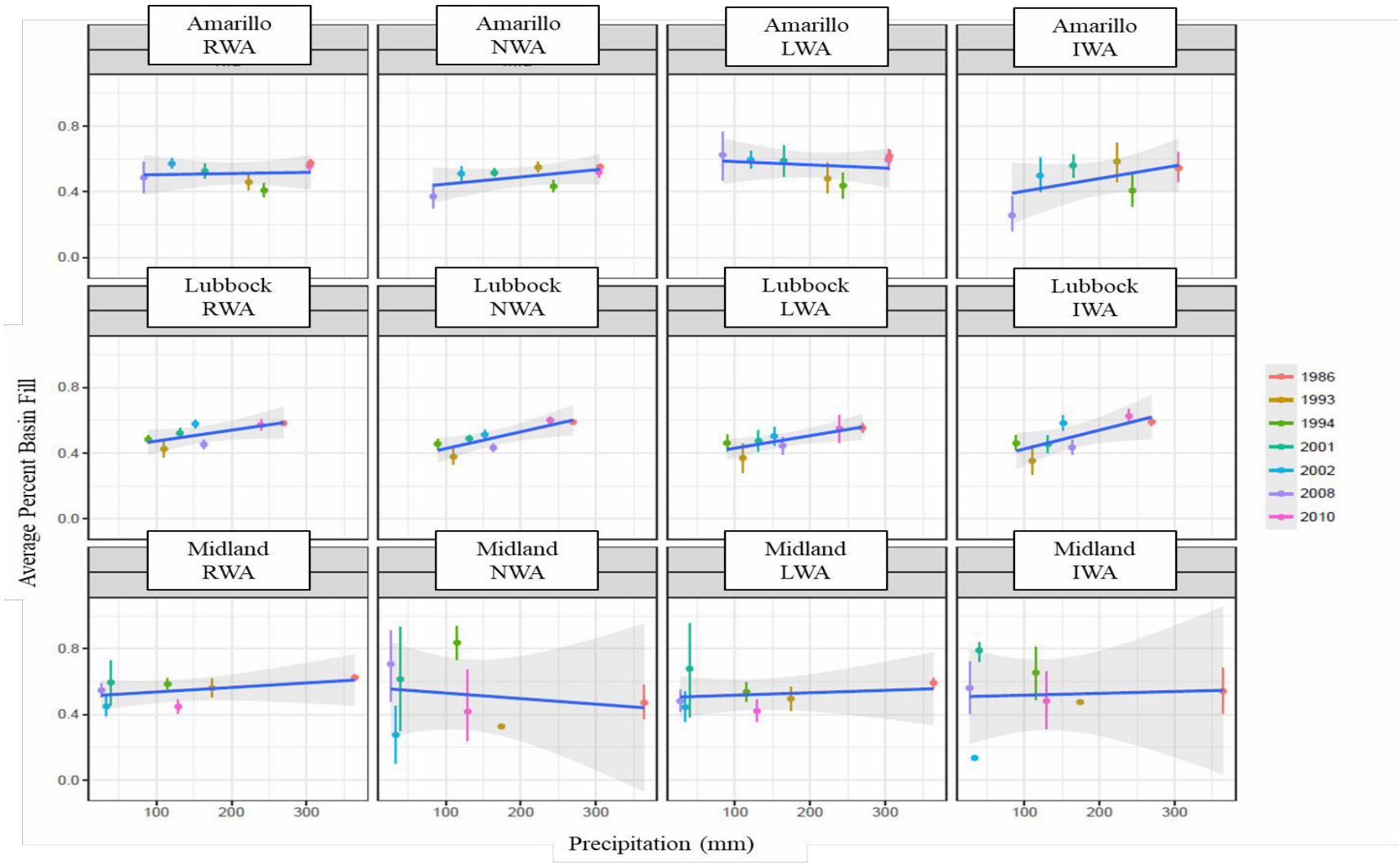

Figure 2.9. Bootstrapping with 95% confidence intervals examining the effects of average percent basin fill as a function of 3-month accumulated precipitation across categories and NOAA National Centers for Environmental Information locations.

Supplementary Material. Statistical test results.

ANOVA & Tukey's HSD results assessing the influence of basin size on surface well relationships.

ANOVA: SINGLE FACTOR						
SUMMARY						
Groups	*Count*	*Sum*	*Average*	*Variance*		
LWA	2514.00	22865.27	9.10	377.34		
RWA	8830.00	60694.29	6.87	179.60		
IWA+NWA	11874.00	96756.13	8.15	103.31		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	13210.68	2.00	6605.34	40.78	< 0.01	3.00
Within Groups	3760522.77	23215.00	161.99			
Total	3773733.45	23217.00				
TUKEY'S HSD TEST						
	P-value	*Assignment*				
LWA vs. RWA	p < 0.01	A				
LWA vs. IWA+NWA	p < 0.01	B				
RWA vs. IWA+NWA	p < 0.01	C				

ANOVA & Tukey's HSD results assessing the influence of surface well features on playa inundation; as measured by percent basin fill, by year (note playa basins with <10% fill were excluded from analysis).

ANOVA: SINGLE FACTOR FOR 1986						
SUMMARY						
Groups	*Count*	*Sum*	*Average*	*Variance*		
LWA	941.00	548.00	0.58	0.07		
RWA	3125.00	1853.58	0.59	0.08		
IWA+NWA	5088.00	2937.10	0.57	0.07		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	0.49	2.00	0.24	3.28	0.04	3.00
Within Groups	682.05	9151.00	0.07			
Total	682.54	9153.00				
TUKEY'S HSD TEST FOR 1986						
	P-value	*Assignment*				
LWA vs. RWA	Non-Significant	NA				
LWA vs. IWA+NWA	Non-Significant	NA				
RWA vs. IWA+NWA	Non-Significant	NA				

ANOVA: SINGLE FACTOR FOR 1993						
SUMMARY						
Groups	*Count*	*Sum*	*Average*	*Variance*		
LWA	118.00	55.79	0.47	0.07		
RWA	364.00	175.14	0.48	0.08		
IWA+NWA	562.00	282.89	0.50	0.08		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	0.15	2.00	0.08	1.02	0.36	3.00
Within Groups	81.00	1041.00	0.08			
Total	81.14	1043.00				
TUKEY'S HSD TEST FOR 1993						
	P-value	*Assignment*				
LWA vs. RWA	NA	NA				
LWA vs. IWA+NWA	NA	NA				
RWA vs. IWA+NWA	NA	NA				

ANOVA: SINGLE FACTOR FOR 1994						
SUMMARY						
Groups	*Count*	*Sum*	*Average*	*Variance*		
LWA	230.00	111.71	0.49	0.07		
RWA	880.00	444.56	0.51	0.07		
IWA+NWA	800.00	366.12	0.46	0.07		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	0.95	2.00	0.47	6.56	< 0.01	3.00
Within Groups	3760522.77	23215.00	161.99			
Total	3773733.45	23217.00				
TUKEY'S HSD TEST FOR 1994						
	P-value	*Assignment*				
LWA vs. RWA	Non-Significant	NA				
LWA vs. IWA+NWA	Non-Significant	NA				
RWA vs. IWA+NWA	$p < 0.05$	A				

ANOVA: SINGLE FACTOR FOR 2001						
SUMMARY						
Groups	*Count*	*Sum*	*Average*	*Variance*		
LWA	90.00	47.46	0.53	0.07		
RWA	546.00	286.90	0.53	0.07		
IWA+NWA	1470	732.56	0.50	0.07		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	0.33	2.00	0.17	2.45	0.09	3.00
Within Groups	142.79	2103.00	0.07			
Total	143.13	2105.00				
TUKEY'S HSD TEST FOR 2001						
	P-value	*Assignment*				
LWA vs. RWA	NA	NA				
LWA vs. IWA+NWA	NA	NA				
RWA vs. IWA+NWA	NA	NA				

ANOVA: SINGLE FACTOR FOR 2002						
SUMMARY						
Groups	*Count*	*Sum*	*Average*	*Variance*		
LWA	276.00	147.81	0.54	0.09		
RWA	1091.00	618.17	0.57	0.08		
IWA+NWA	774.00	404.54	0.52	0.07		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	0.91	2.00	0.46	5.86	< 0.01	3.00
Within Groups	166.72	2138.00	0.08			
Total	167.64	2140.00				
TUKEY'S HSD TEST FOR 2002						
	P-value	*Assignment*				
LWA vs. RWA	Non-Significant	NA				
LWA vs. IWA+NWA	Non-Significant	NA				
RWA vs. IWA+NWA	$p < 0.05$	A				

ANOVA: SINGLE FACTOR FOR 2008						
SUMMARY						
Groups	*Count*	*Sum*	*Average*	*Variance*		
LWA	175	82.70	0.47	0.06		
RWA	652.00	313.32	0.48	0.07		
IWA+NWA	765.00	330.59	0.43	0.06		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	0.88	2.00	0.44	6.84	< 0.01	3.00
Within Groups	101.76	1589.00	0.06			
Total	102.64	1591.00				
TUKEY'S HSD TEST FOR 2008						
	P-value	*Assignment*				
LWA vs. RWA	Non-Significant	NA				
LWA vs. IWA+NWA	$p < 0.05$	A				
RWA vs. IWA+NWA	$p < 0.05$	B				

ANOVA: SINGLE FACTOR FOR 2010						
SUMMARY						
Groups	*Count*	*Sum*	*Average*	*Variance*		
LWA	181.00	95.42	0.53	0.07		
RWA	739.00	397.70	0.54	0.09		
IWA+NWA	1288.00	748.01	0.58	0.09		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	1.09	2.00	0.54	6.41	< 0.01	3.00
Within Groups	187.75	2205.00	0.09			
Total	188.85	2207.00				
TUKEY'S HSD TEST FOR 2010						
	P-value	*Assignment*				
LWA vs. RWA	Non-Significant	NA				
LWA vs. IWA+NWA	p < 0.05	A				
RWA vs. IWA+NWA	Non-Significant	NA				

CHAPTER III

QUANTIFYING THE EFFECTS OF PROJECTED URBAN GROWTH ON CONNECTIVITY AMONG WETLANDS IN THE GREAT PLAINS (USA).

Introduction

Urban ecosystem studies have traditionally focused on large metropolitan centers. However, urbanization can produce a variety of environmental changes that have ripple effects along the urban-rural continuum (McDonnell & Pickett, 1990). Although popular, the concept of the urban-rural continuum itself is subject to changes both social and political (Lichter & Ziliak, 2017) as well as ecological (Geneletti, La Rosa, Spyra & Cortinovis, 2017; Hansen et al., 2005).

Moreover, urban periphery studies may assist future planning and sustainability efforts by managers (Geneletti et al., 2017; La Rosa, Geneletti, Spyra, & Albert, 2017). Therefore, since the effects of urbanization can occur across a wide range of habitats and at several levels simultaneously, stakeholders and managers are increasingly interested in studies of "rural urbanization." Studies of rural urbanization can inform regional conservation practices, ecosystem service management, and environmental hazard response (Cutter, Ash, & Emrich, 2016; Oliver & Thomas, 2014; Vias, 2010; Walker, de Beurs, & Henebry, 2015). Rural urbanization ecological studies will be especially important for those regions facing increasing demographic pressures and climate change-induced restrictions to large-scale management actions.

The Great Plains, an approximately 1.4-1.9 million km^2 expanse of arid and

semi-arid prairies, grasslands, and steppes of the North American continental interior (Samson & Knopf, 1994), represents just such an area ripe for non-traditional, rural urban ecological studies.

Although the Great Plains are known derisively as "flyover country," this region is one of the world's leading agricultural production areas, with several historic periods of population shifts of settlement abandonment as well as urban expansion (Kotkin, 2012; Wishart, 2004). The Great Plains has experienced a recent surge in economic and population growth, attributed to energy resource development, increased agricultural production, and favorable economic conditions (Kotkin, 2012; Scott, 2017; U. S. Census Bureau, 2013; U. S. Census Bureau, 2014). However, these regional trends may be variable at local scales, with some areas of the Great Plains experiencing population declines (Wishart, 2004; Parton, Gutman & Ojima, 2007). Despite these potentially contrasting socio-economic influences, recent effects (Kotkin, 2012; Scott, 2017; U.S. Census Bureau, 2013; U. S. Census Bureau, 2014) have resulted in increased amounts of impervious surface coverage and expansion of developed land usage both within and surrounding regional urban centers in the Great Plains. As a consequence of these local landscape changes, a yet-unknown number of regional wetlands are also subject to increases in surrounding impervious surface and expansion of developed land usage.

Just as we do not normally view the Great Plains as urban, neither do we typically think of it as being wet. However, the Great Plains contains millions of freshwater wetlands that form an ecological network of wildlife habitat, the

Central Flyway for migratory birds (Smith, Pederson, & Kaminski, 1989; Tiner, 2003). This continental-scale migratory wildlife corridor links the glacially formed prairie potholes of the northern Great Plains to the aeolian wetlands of the central and southern Great Plains, known as playas (Bolen, Smith, and Schramm Jr., 1989; Guthery & Bryant, 1982; McIntyre et al., 2014). The playas of the Great Plains of the United States are similar to other networks of ephemeral wetlands in an otherwise arid landscape that are vulnerable to effects of land-use and climate changes, such as the sabkhas of north Africa (Briere, 2000) and playas of inland Australia (Bourne & Twidale, 2010). Projected climatic and development patterns for the Great Plains will further alter the landscape in terms of its composition, configuration, and connectivity among the 89,798 playas of the region (Fig. 3.1). Investigating future patterns of rural urbanization and associated impacts on playa wetlands can inform management actions to more sustainably mitigate climatic and development effects within the Great Plains.

Playas are the primary source of aboveground freshwater for the central and southern Great Plains, making them regional biodiversity hotspots through provision of critical resources for aquatic and amphibious wildlife (Bolen et al., 1989; Hall et al., 2004; Haukos & Smith, 1994; Hernandez, Reece, & McIntyre, 2006; Ramesh, Griffis-Kyle, Perry, & Farmer, 2012; Tsai, Venne, McMurry, & Smith, 2012), and the primary sources of groundwater recharge for the Ogallala Aquifer (Gurdak & Roe, 2010; Smith, 2003). Playas have been modified for stormwater management and recreation in urban areas

(Collins et al., 2014; Haukos & Smith, 1994; Heintzman, Anderson, Carr, & McIntyre, 2015); these alterations are expected to increase with expanding urbanization projected for the Great Plains region. Playas are fed from precipitation runoff, making them sensitive to weather and to human land-use decisions that alter watershed structure (Smith, Tsai, Cox, Smith, & McMurry, 2011; Smith, 2003).

Great Plains wetlands are being altered by human land use, including urbanization, and by climate change. However, these drivers do not always impair function: urban playas often have prolonged hydroperiods (up to 1312 days; Collins et al., 2014) relative to non-urban ones (up to 453 days; Venne, Tsai, Cox, Smith, & McMurry, 2012; Tsai, Venne, McMurry, & Smith, 2007) as a result of anthropogenic inputs of water and basin modifications for long-term water retention (Collins et al., 2014; Ganesan et al., 2016; Uden et al., 2015; VanLandeghem, Meyer, Cox, Sharma, & Patino, 2012). Additionally, playas within developed areas differ from non-urbanized playas in terms of water chemistry and their microbial community (Durham, Porter, Webb, & Thomas, 2016; Heintzman et al., 2015; Moorhead, Davis, & Wolf, 1998; Starr, Heintzman, Mulligan, Barbato, & McIntyre, 2016; Warren, Jeter, Kimbrough, & Zak, 2004), yet during drought, playas in developed areas may be the only ones containing water (Collins et al., 2014), so their reliability may allow them to play an unexpectedly positive role in terms of supporting landscape connectivity (Ruiz et al., 2014). Although the biological productivity of playas is driven by their natural wet-dry cycling (Haukos & Smith, 1994), the prolonged hydroperiod of urban playas may facilitate the development or

dispersal of some species (Collins et al., 2014; Venne et al. 2012). Thus, urban playas are habitats that entail regional ecological trade-offs for managers as to whether to prioritize more natural ecosystem functionality or to prioritize prolonged aquatic habitat persistence across the landscape, the latter of which may be especially important during times of drought (Collins et al., 2014) and for migratory species.

The importance of playas as migratory stopover sites is well-recognized (McIntyre et al., 2014; Smith, 2003; Tiner, 2003), but the ecological network of playas is dynamic and subject to continued anthropogenic alterations. Interannual differences in precipitation and land use generate different topologies of wet playa occurrence from year to year (Ruiz et al., 2014). The consequences of these different topologies for wildlife migrating through the network have rarely been considered. Given regional climate change projections and increased likelihood of drought in the Great Plains, urban playas with their prolonged hydroperiods may be of increasing importance to migratory route connectivity. Despite the importance of playas for wildlife and humans, limited knowledge exists on current and expected rates of playa urbanization (i.e., the transformation of playas that do not exist in an urban context to those that do, and/or playas that are expected to experience increased ecological alterations as a result of anthropogenic pressures associated with urban development), which is needed for regional planners and private stakeholders to mitigate land-use and climatic changes on the Great Plains, especially with respect to landscape connectivity for wildlife.

For our study we documented projected increases in playa urbanization and subsequent changes to wetland connectivity using data developed by the U. S. Environmental Protection Agency's Integrated Climate and Land-Use Scenarios (ICLUS; https://www.epa.gov/iclus) and the U. S. Geological Survey's FOREcasting SCEnarios of land-use change model (FORE-SCE; http://landcarbon.org/categories/land-use/download/) (Bierwagen et al., 2010, U.S. EPA, 2010; Sohl, Sayler, Drummond, & Loveland, 2007). These models generate climate and land-use projections and have been used to quantify projected urban growth (Bierwagen et al., 2010; Caldwell, Sun, McNulty, Cohen, & Moore Myers, 2012; Georgescu, 2015; Georgescu, Morefield, Bierwage, & Weaver, 2014; Mondal, Butler, Kittredge, & Moser, 2013; Reinman, Hutyra, Trlica, & Olofosson, 2016; Sohl et al., 2012; Sohl et al., 2016). From these models we derived projected trajectories of impervious surface and developed land use. These trajectories were then used to examine potential alterations within the ecological network of prairie wetlands via a graph theory approach quantifying topological characteristics of the Great Plains playa network (Bunn, Urban, & Keitt, 2000; Calabrese & Fagan, 2004; Minor & Urban, 2007; Minor & Urban, 2008; Urban & Keitt, 2001). Overall, we predicted that ICLUS models based on impervious surface coverage (as a continuous variable) would result in the largest number of urban playas and thus correspond with higher connectivity values (both in terms of overall network structure and importance of individual wetlands) than those that used FORE-SCE models (with its static, majority-rule classification scheme). We

were guided to this prediction based on the observation that impervious surface development (e.g. roads) can occur at any point along an urban-rural gradient. Because landscape connectivity underpins species persistence, managing for connectivity is important in landscape and urban planning (Fahrig, 2003; Taylor, Fahrig, Henein, & Merriam, 1993; Traktenbrot, Nathan, Perry, & Richardson, 2005), so our overall objectives were to quantify connectivity among urban playas under a range of potential futures, and to identify any wetlands that were consistently identified across models and climate scenarios as being affected in future as good candidates for connectivity conservation.

Methods

Data

Our focal region was based on the digital playa wetland features contained within the Maps of Probable Playas (MPP) database developed by the Playa Lakes Joint Venture (http://pljv.org/for-habitat-partners/maps-and-data/maps-of-probable-playas/, accessed May 2016). This database mapped 89,798 playa wetlands across ~68 million ha of the U. S. portion of the Great Plains in Colorado, Kansas, Nebraska, New Mexico, Oklahoma, and Texas. Within the MPP, an individual playa basin may have multiple units as a result of the presence of multiple within- basin sub-features (Fig. 3.2). Some of these features are natural (e.g. presence of open water in one portion of a basin and presence of woody wetland vegetation in another portion of the same basin resulted in two wetland classification types within the same unique basin ID in the MPP), and others are due to human activity (e.g. a road bisecting a playa). Each sub-feature within a basin was treated as a separate analysis unit because each sub-feature has unique hydrological properties (e.g. hydroperiod). This approach also better reflects real-world conditions and more accurately

reflects habitat availability constraints on wildlife.

We used ICLUS and FORE-SCE models to determine the extent, type, and rate of playa urbanization across the Great Plains playa region. ICLUS' primary focus is on changes in impervious surface coverage and population growth changes, whereas FORE-SCE's is on changes in land use. Impervious surface and developed land use are both associated with urban growth but are not synonymous with each other: for example, a rural highway has impervious surface but may not be associated with developed land use, and a developed area can have relatively little impervious surface (e.g. due to the presence of parks and vacant lots). Impervious surface and developed land use adjacent to or near playas have been shown to affect playa hydrology, water quality, and biota through changes in water flow, water chemistry, and other proximal drivers (Collins et al., 2014; Heintzman et al., 2015; Starr et al., 2016). Although the effects of impervious surface are not necessarily the same as those of developed land use (impervious surface may increase runoff, for example, whereas some forms of land use may disrupt runoff and increase water infiltration), these two features are defining traits of urbanized landscapes (Alberti, 2005; Arnold & Gibbons, 1996). Using both ICLUS and FORE-SCE thus allowed us to perform a more comprehensive estimate of playa urbanization trajectories than examining either dataset alone.

Both ICLUS and FORE-SCE models were developed from Intergovernmental Panel on Climate Change (IPCC) Special Report on Emission Scenarios (SRES) storylines for the continental United States and were developed during

the early part of the current decade. We therefore used commensurate pairings between the ICLUS climate scenarios A1, A2, and B1 and the FORE- SCE climate scenarios A1B, A2, and B1, respectively, to represent a range of possible future conditions. These pairings are broadly consistent across both models (Sohl et al. 2012) and can be adapted to more recent IPCC Representative Concentration Pathways (RCP) climate scenarios (Moss et al., 2010; van Vuuren et al., 2011). Although the RCP scenarios are not exactly equivalent to the older SRES scenarios used in ICLUS and FORE-SCE, there are similarities with respect to emissions, concentrations, and temperatures (U.S. Global Change Research Program, 2014). For a detailed conversion between IPCC climate scenarios, see Rogelj, Meinshausen, & Knutti (2012). To develop comprehensive estimates of future urban playa development, we compared projected changes in impervious surface coverage from ICLUS and developed land use from FORE-SCE under all three of the climate-change scenarios (Table 3.1). Our analysis used a baseline year of 2020 and projected to 2050 to analyze future playa development trajectories; we used these years due to the decadal timeframe of ICLUS projections and because 2050 represents the latest available projection of FORE-SCE.

Data Processing and General Workflow

For each of the three ICLUS impervious surface raster datasets (under climate scenarios A1, A2, and B1), data were resampled in ArcGIS 10.3 (Redlands, CA) to match the cell sizes in the three FORE-SCE land-use change raster datasets (A1B, A2, B1). The data from ICLUS were only available at a 1 km

resolution whereas data from FORE-SCE were only available at 250 m; we thus had data with two different grain sizes that we resampled to align the resolutions for spatial analysis in ArcGIS. We resampled the coarser-grained ICLUS data to match the finer-grained FORE-SCE data (dividing larger cells to match the size of the smaller ones) rather than the reverse (merging smaller cells to match the size of the larger ones). To do so, we divided each original 1000 m x 1000 m ICLUS cell to create four identical 250 m x 250 m cells that covered the same extent as the original ICLUS cell. Although rescaling from smaller to larger may be applicable to some studies, our raster resampling method allowed for a more detailed depiction of urban development of playa wetlands via expansion of both impervious surface and urban land use. Our rationale for our choice (resampling ICLUS to match FORE-SCE, i.e., resampling larger cells to create smaller ones) was based on preserving data integrity that can be lost when merging smaller cells to create larger ones (see Turner, O'Neill, Gardner, & Milne, 1989 for more information). This resampling did not introduce false precision into the analysis, because values from the rasters were extracted to wetland centroids.

Both raster layers and the MPP layer were spatially projected to UTM Zone 13N. ICLUS and FORE-SCE data were then clipped to match the extent of the MPP. The MPP native polygon data were then converted to point data, and centroid coordinates of each playa were determined for subsequent connectivity analyses. The resulting layer thus contained imperious surface and land-use data for each of the 89,798 playa features in the MPP for each of

the three ICLUS and three FORE-SCE datasets. This layer was then queried using the Select by Attributes Tool to determine individual playas trajectories in impervious surface coverage and projected land use (Fig. 3.3). Designation of a playa as urban was thus based on the single cell value (land-use type or percent impervious surface) at a cell centroid for each of the ICLUS and FORE-SCE models.

Because our objectives were to investigate the role that urban expansion will have on playa wetlands and thence on their contribution to connectivity, we quantified connectivity only among those playas expected to be impacted by current or future urban growth. By not including the ~99% of playas that do not exist within an urban context, we were able to focus on our targeted habitat type. Non-urban playas do play important roles in connectivity (Albanese & Haukos, 2016); however, they are dry far more often than they are wet (Johnson et al., 2011). Because playas surrounded by urban land use have longer hydroperiods than do playas with other forms of land cover in their watersheds (Collins et al., 2014), urban playas represent actual potential habitat for aquatic and wetland-associated species within an arid region. As such, urban playas have been shown to play an outsized role in overall connectivity through the playa network, relative to non-urban ones (Collins et al., 2014; Ruiz et al., 2014). Therefore, we identified and examined only those playas projected to experience urban development in terms of (1) any increase in impervious surface coverage under each climate scenario (i.e., playa centroids within raster cells projected to increase in impervious surface)

(ICLUS); (2) those projected to experience an increase in developed land use under each climate scenario (i.e., playa centroids projected to occur within a raster cell that exists within or transitions to developed land use) (FORE-SCE); and (3) a consensus model that identified playas projected to experience an increase in both impervious surface and developed land use (i.e., playas centroids in cells that increase in impervious surface and occur within developed land use) (both ICLUS and FORE- SCE). Comparing projections from both models in this way provided the opportunity for identification of playas affected, regardless of model, for future landscape-planning activities across a range of potential development pathways. This resulted in the ICLUS Model Network, which identified all playas in the MPP that are expected to experience an increase in surrounding impervious surface coverage among each of the ICLUS climate scenarios by 2050; the FORE- SCE Model Network, which depicted all playas in the MPP that are expected to exist within urban land use among each FORE-SCE climate scenario by 2050; and the Consensus Model Network, which depicted those playas projected to experience an increase in impervious surface coverage and exist within classified developed land use by 2050 among all ICLUS and FORE- SCE climate scenarios. Since each of these model networks were built from the MPP (which natively contained basin size information), we were able to examine whether significant differences were projected among networks on the basis of playa size using the statistics tool in ArcGIS 10.3, followed by analysis of variance (ANOVA) in SAS 9.4 (Cary, NC). Significant ANOVA

models were then followed with a Fisher's Least Significant Difference test of means.

Connectivity Analyses

Using graph theory-based terminology, each of these three modeled networks consisted of nodes (i.e., playa centroids) and the links (i.e., Euclidian distances) between them; connectivity among the nodes was examined for each of the three networks. Connectivity was quantified for each of the three model networks using methods derived from Ruiz et al. (2014) with the *igraph* package (Csardi & Nepusz, 2006) in R 3.3.2 (R Development Core Team, 2014). We compared the networks using seven graph theory metrics pertaining to size and connectance. Four of these metrics quantified the network as a whole whereas the other three metrics defined the roles of individual playas within each network. The four whole-network metrics were (1) coalescence distance (threshold distance at which the network becomes connected into a single cohesive grouping of nodes; this distance may be thought of as the farthest distance between neighboring nodes an organism must travel to traverse the network); (2) graph density (bidirectional linkage density, or the ratio of links present to the number of all possible links among nodes); (3) average nodal connectance (number of connections that a node has with other nodes at coalescence; known as average path length in *igraph*, higher values of this metric indicate more path redundancy through the network); and (4) graph diameter (the number of links forming the longest path through the network).

The metrics investigating individual playas included the degree to which each node in each network played a role as a (5) stepping-stone that facilitates connectivity among habitat patches, (6) hub that is connected to more patches relative to other patches or (7) cutpoints that with removal would increase network fragmentation (increase coalescence distance). Stepping-stones are those nodes with high values of betweenness centrality, which is highest for those nodes along the most direct paths through a network. Hubs were identified as having high Kleinberg's centrality scores, which quantifies the relative number of links per node. Finally, cutpoints (articulation points in *igraph*) are those nodes that, if removed, fragment the network into clusters that are farther apart that the previously identified coalescence distance. For these three individual-node metrics, we identified and mapped the distribution of the top 10 stepping-stones, top 10 hubs, and all cutpoints (Drake, Griffis-Kyle, & McIntyre, 2017; McIntyre, Drake, & Griffis-Kyle, 2016; Ruiz et al., 2014). Because a network is defined solely by its nodes and links, the global connectivity metrics are indicators of properties of one or both of these and as such are somewhat correlated (e.g. average node connectance is positively associated with the number of links). The individual-scale metrics, however, are based upon their placement within the network and as such are only obliquely related to the global metrics. Therefore, using both global and individual metrics provided a more comprehensive examination of the playa network.

Results

Overall Results

A side by side comparison of differences in expected urban playa locations by 2050 in relation to large urban centers reveals the unique connectivity structure of each of the model networks (Fig. 3.4).

Both ICLUS and FORE-SCE projected increased urbanization in the south-central Great Plains, with amounts differing by model and climate scenario. Between the years 2020 and 2050, average impervious surface coverage surrounding all playas was projected to increase in the ICLUS scenarios A1 (by 0.03% over all 89,798 playas), A2 (0.03%), and B1 (0.02%). Total developed land use for the entire playa region was also projected to increase in each of the FORE-SCE scenarios A1B (by 0.0054% or 19,604.00 km^2 over the entire playa region as depicted in Fig. 3.4), A2 (0.005% or 17,731.50 km^2), and B1 (0.0037% or 13,504.50 km^2).

However, these increases in projected impervious surface coverage and developed land use were not completely concordant among scenarios or models: some playas are expected to experience a projected increase in surrounding impervious surface yet not be classified within developed land use. Similarly, playas may be projected to occur within developed land use yet not experience an increase in surrounding impervious surface (Table 3.2).

Furthermore, assays of playa size differences and structural connectivity among the scenarios depicted vastly different playa network topologies during the same time span. Despite the overlap in ranges of basin sizes among model

networks (Table 3.3), the ICLUS Model Network contained playas that were significantly larger than those in either the FORE-SCE Model Network or the Consensus Model Network (Fisher's LSD, $p = <0.0001$). However, there was no significant difference in basin sizes between the FORE-SCE Model Network and the Consensus Model Network. With respect to structural connectivity, differences among network models were especially pronounced for metrics evaluating coalescence distance, graph density (Table 3), and the distribution of stepping-stones, hubs, and cutpoints (Supplementary Material).

ICLUS Model Network

A total of 795 playa features within 626 basins were projected to experience an increase in impervious surface coverage between 2020 and 2050 in all three climate scenarios. These 795 playa features had an average basin size of 3.35 ha (range: 0.05 – 47.30 ha) and were located in Texas (660 playa features), Colorado (108), Kansas (26), and Oklahoma (1). The ICLUS Model Network was characterized by a couple of dense groupings of playas (along the Front Range of Colorado to the north, and a larger cluster south of the Arkansas River). Of the three modeled networks (ICLUS, FORE-SCE, and Consensus), this one had most nodes and links. Although we predicted that this network would have the most nodes, the coalescence distance of this network was not the shortest. Graph density was larger but average node connectance and graph diameter were smaller than for the FORE-SCE Model Network. (Table 3.3). The top 10 stepping-stones were concentrated in the larger southern cluster, with two stepping-stones also functioning as cutpoints (located in the towns of

La Junta, Colorado, and Boise City, Oklahoma) connecting the northern and southern clusters. A third cutpoint was present within the northern cluster, linking a single playa in far eastern Colorado near the town of Holyoke. The top 10 hubs were highly concentrated in the region with the greatest density of playas in the Texas Panhandle (Fish, Atkinson, Mollhagen, Shanks, & Brenton, 1998) in the southern cluster (Fig. 3.5).

FORE-SCE Model Network

A total of 420 playa features within 353 basins were projected to exist within developed land-use by 2050 in all three of the climate scenarios. These 420 playa features had an average basin size of 2.22 ha (range: 0.01 – 45.27 ha) and were located in Texas (296), Colorado (55), Kansas (36), Nebraska (25), New Mexico (6), and Oklahoma (2). The urban playas forecast under FORE-SCE form a diffuse network, unlike the denser network from ICLUS. Contrary to our predictions, the FORE-SCE Model Network featured the lowest coalescence distance, despite having the second- fewest numbers of playas and linkages. These fewer playas were more diffusely spread, resulting in a lower graph density and larger graph diameter than the ICLUS network (Table 3.4). This network had the highest average nodal connectance of any of the three networks, indicating the highest amount of path redundancy. The top 10 stepping-stones, top 10 hubs, and all of the cutpoints were different playas than in the ICLUS Model Network. The stepping-stones occurred primarily in Nebraska, Oklahoma, and the northern Texas Panhandle. A smaller group of

stepping-stones also connected western Oklahoma with New Mexico and Colorado. Two cutpoints linked playas in far eastern Nebraska with the main network. The top 10 hubs were concentrated near the southwestern periphery of the network in New Mexico and Texas (Fig. 3.6).

Consensus Model Network

The consensus network of playas that will be influenced by urbanization and climate change was comprised of a north-south line of playas positioned around existing cities and towns in Texas and Kansas, and ones associated with the Denver (Colorado) metropolitan area. These 126 playa features within 93 basins were projected to experience an increase in surrounding impervious surface coverage and developed land-use by 2050, regardless of climate scenario. Averaging 2.25 ha (range: 0.07 – 13.41 ha), they were located in Texas (110), Colorado (15), and Kansas (1). Because this network had the fewest nodes and links, it is not surprising that it had the greatest coalescence distance and lowest average nodal connectance. The top 10 stepping-stones were concentrated in Texas in the vicinity of Lubbock. The top 10 hubs were all located in Texas in the southern cluster, mostly near the relatively large population centers of Amarillo, Midland, and Odessa. One hub occurred in extreme northern Texas near the town of Spearman. Cutpoints were observed near Garden City, Kansas, and Gleneagle, Colorado (Fig. 3.7). These consensus stepping-stones, hubs, and cutpoints are the most appropriate candidates for management, as they are the most likely to be influenced by

urban growth regardless of focus (impervious surface or land use) or climate scenario.

Discussion

Urban playas represent important ecological (Collins et al., 2014; Ruiz et al., 2014; Starr et al., 2016) and cultural resources (Smith, 2003; Young, 2015). Although urban playas have garnered some scientific interest with respect to their contamination chemistry (Arefeen, 1995; Faust et al., 2012; Heintzman et al., 2015; Huang, 1992) and microbial communities of human health concern (Huddleston, Zak, & Jeter, 2006; Moorhead et al., 1998; Warren et al., 2004), our study is the first to our knowledge to document quantitatively the projected rates and distribution of future playa urbanization and their associated influence on network connectivity under various climate and land-use change scenarios. Such scenarios are also in play for ephemeral wetland networks in other parts of the world.

With respect to playa management, climate-mitigation actions are intractable for much of the Great Plains playa region, but what can be managed more effectively is land-use change, including urban growth. Focusing on impervious surface is one way to project urban growth; using developed land use is another. These two ways do not converge upon similar outcomes in terms of which playas will be considered urbanized, however. Both small-scale changes in impervious surface development (road construction), and larger-scaled, municipal projects (urban parks development) will increase the number

of playas that are urbanized, which will influence individual playa ecology (i.e., hydrology, habitat quality, and biotic communities) and overall playa network structure (i.e., routes through the landscape based on the topological distribution of hubs, stepping-stones, and cutpoints). Because urban playas are more consistently inundated compared to non-urban playas, especially during drought (Collins et al., 2014), the distribution of urban playas may foster channelization of migratory movement pathways across the network (due to the presence of fewer options rather than the more diffuse full network of playas), as drought conditions are projected to occur more frequently within the region (McIntyre et al., 2014).

Urban playas, with their characteristic hydrology, biotic communities, and municipal importance, are expected to play important roles as stepping-stones, hubs, and cutpoints in supporting movement through this wetland network in the future. However, the ability of urban playas to function in these roles is influenced by the biotic constraints of species that use the system and the topology of the network as a whole. With coalescence values ranging from 189 – 364 km, the distances among urban playas may be insurmountable for some species (e.g. amphibians) yet be accessible for others (e.g. migratory birds). Also of importance is the spatial arrangement of playas within the network; as predicted, the ICLUS Network Model had the greatest number of nodes, but the FORE-SCE Network Model had the greatest average nodal connectance (i.e., greatest path redundancy), a potentially important component of local habitat selection for migratory species. Lastly, and with respect to both graph

density and graph diameter, linkages were depicted as Euclidean, but the actual movements of species will likely not be (Albanese & Haukos, 2017; Drake, Griffis-Kyle, & McIntyre, 2017; Haig, Mehlman, & Oring, 1998; Pittman, Osbourn, & Semlitsch, 2014; Smith & Green, 2005; Sinsch, 2014), further complicating management actions.

Because our study examined connectivity within the network of playas expected to be directly affected by urbanization, which are <1% of the total number of all playas in the Great Plains, our results are best viewed as highly conservative with respect to overall potential connectivity changes that are anticipated to occur within this region. However, while other studies have described connectivity of the playa network as a whole in other contexts (Albanese & Haukos, 2017; McIntyre et al. 2018; Ruiz et al. 2014), these assessments did not examine land use, nor future projections of land use and climate change. Although the overall number of playas expected to experience future urbanization is small, those playas that are so affected may exert ecological influences at larger spatial extents than would be immediately inferred by their abundance on the landscape.

Relatedly, our results suggest that effects of urbanization may differ by playa basin size. In the ICLUS Network Model, larger basins were expected to be incorporated into urban environments, whereas the FORE-SCE Network Model and Consensus Model Network predicted urbanization of smaller playas. Because urban development and basin size differences can prolong playa hydroperiod, urban playas may represent an attractive opportunity and

effective target to mitigate against anticipated climate changes (Hayhoe & Wuebbles, 2007; U. S. Global Change Research Program, 2014) by maintaining accessible aquatic resources on the landscape, albeit at the potential reduction in regional productivity of playas (Haukos & Smith, 1994). Potential effects of compromised urban water quality on these events, and decreased ecological functionality of smaller playas via development, however, remain to be examined.

The ecological threats posed by urbanization and climate change to playa network functionality are similar to those affecting isolated wetland systems worldwide (Calhoun et al., 2017; Cohen et al. 2016; Rains et al., 2016), with both urban development and climate change expected to accelerate in the foreseeable future. Indeed, an examination of recent aerial imagery of urban development in the Great Plains playa region has revealed that several playas that we included in our models have already been effectively removed from the landscape, being replaced entirely by built-up areas. Unfortunately, direct mitigation practices for threats associated with urbanization is scant, based on limited legal protections of playas (Haukos & Smith, 2003). The future trajectories of urbanizing playas will be influenced by both economic factors (municipal land acquisition and zoning) and social factors (preferences for conservation and park spaces), which are themselves subject to change across the urban environments of the Great Plains and thus are outside the realm of this study. However, our research can inform ecologists and mangers about playa conservation under a suite of climate and development scenarios, by

identifying exactly which playas are likely to be affected by additions of impervious surface, land-use development, or both (Supplementary Material). Additionally, our results can be used to identify and direct the establishment of sites to better review the effects of rural urban development, a potentially fruitful application of urban ecological principles and landscape planning. Finally, the 126 Consensus Model Network playa features are the best candidates for longitudinal monitoring of the effects of future urban growth on aquatic ecosystems in the Great Plains because they are likely to be affected by urbanization regardless of how that is defined. Geographic coordinates of these playas are provided in the Supplementary Material. These playas will likely show impacts from growth in both impervious surface and developed land-use, which could be compared to patterns in playas that are predicted to be affected by only one of the variables. For the majority of the urban playas, the two projection models did not converge; therefore, a more targeted approach to urban playa management will be needed for these other playas by first identifying the more likely changes to occur for a given locality (impervious surface expansion or land-use development), which would then allow one to focus on the projected outcomes from the appropriate model (ICLUS or FORE-SCE). By comparing patterns that emerge from the Consensus Model Network playas with those from the ICLUS and FORE-SCE Model Network playas, we may be able to tease apart which defining feature of urbanization—impervious surface or development—is the more influential. Our findings are, essentially, predictions that need to be tested.

Conclusions

Playas in urban contexts, as a consequence of their altered hydrology, may in the future become increasingly important and consistent components in maintaining regional connectivity under projected climate and land-use changes in the Great Plains (Burris & Skagen, 2013; Hayhoe & Wuebbles, 2007; McIntyre et al., 2014). The Great Plains playa wetland network has been and will continue to be altered by the coincident challenges of land-use and climate changes; however, the projected distribution and degree of the effects of these changes are subject to model inputs and may not reflect on the ground decision-making by stakeholders. Since urbanization makes playas more likely to contain water, enhancing connectivity in this region may involve embracing urban development, which is a rather novel concept and one that is contrary to traditional conservation thinking. Our study can be used to inform the actions of stakeholders and guide larger-scale landscape planning. The current existence and expected increases in both the number and distribution of urban playas has resulted in altered ecological function of the playa network and may yet provide opportunities for mitigation of some climate based management practices both at local and regional scales. Thus, although our study is limited to discussion of urban playas, it provides a basis by which to better appreciate the connectivity difficulties put forth by urbanization and climate change. All future landscape modelling is subject to uncertainty; however, by identifying which playas are most likely to be affected by projected landscape changes, our findings can be used to help guide regional development and conservation strategies across the Great Plains. Finally, our study emphasizes that a broader appreciation of urban ecology is needed, focusing not just on traditionally large urban areas, because even small or modest

changes in impervious surface or developed land use may have large effects in rural urban areas.

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Table 3.1. Description of ICLUS v 1.3.2 and FORE-SCE climate models and their approximate IPCC SRES and IPCC RCP equivalents. "N/A" = not applicable because no equivalent value.

IPCC RCP	**IPCC SRES**	**ICLUS** **(SRES Storylines)**	**FORE-SCE** **(SRES Storylines)**
8.5	A1f	A2	A2
6.0	A1B	A1	A1B
4.5	B1	B1	B1
2.6	N/A	N/A	N/A

Table 3.2. Summary of differences in landscape contexts for urban playa features within the ICLUS Model Network, the FORE-SCE Model Network, and the Consensus Model Network. A1*, A2*, and B1* are naming conventions to delineate the combined climate models for the Consensus Model Network. The proportion of playas affected by a given scenario and year are the numbers of playas present for a given scenario and year divided by the total number of playas predicted by 2050 to be affected.

	ICLUS Model Network (795 playa features)					
Scenario	A1		A2		B1	
Year	2020	2050	2020	2050	2020	2050
Average % of Surrounding Impervious Surface Among Playa Features In A Network (*Ranges*)	5.21 *(0.01-41.71)*	7.20 *(0.35-51.85)*	4.90 *(0.01-37.48)*	7.31 *(0.36-51.85)*	4.97 *(0.01-37.48)*	6.59 *(0.35-44.37)*
% of Playas in Developed Land Use (*Number of playas*)	16.1 *(128)*	24.0 *(191)*	16.1 *(128)*	21.9 *(174)*	14.7 *(117)*	18.6 *(148)*
	FORE-SCE Model Network (420 playa features)					
Scenario	A1B		A2		B1	
Year	2020	2050	2020	2050	2020	2050
Average % of Surrounding Impervious Surface Among Playa Features In A Network (*Ranges*)	8.84 *(0.00-51.85)*	9.97 *(0.00-48.04)*	8.53 *(0.00-41.71)*	9.73 *(0.00-51.85)*	8.81 *(0.00-41.71)*	10.12 (0.00-51.85)
% of Playas in Developed Land Use (*Number of playas*)	86.9 *(365)*	100.0 *(420)*	89.8 *(377)*	100.0 *(420)*	83.3 *(350)*	100.0 *(420)*
	Consensus Model Network (126 playa features)					
Scenario	A1*		A2*		B1*	
Year	2020	2050	2020	2050	2020	2050
Average % of Surrounding Impervious Surface Among Playa Features In A Network (*Ranges*)	13.51 *(0.53-36.61)*	16.71 *(0.63-44.37)*	12.93 *(0.36-36.61*	16.40 *(0.63-44.37)*	13.37 *(0.53-36.61)*	16.72 *(0.63-41.87)*
% of Playas in Developed Land Use (*Number of playas*)	85.7 *(108)*	100.0 *(126)*	90.4 *(114)*	100.0 *(126)*	82.5 *(104)*	100.0 *(126)*

Table 3.3. Summary of differences in average basin size and connectivity metrics for urban playas within the ICLUS Model Network, the FORE-SCE Model Network, and the Consensus Model Network by 2050.

	ICLUS Model Network	**FORE-SCE Model Network**	**Consensus Model Network**
# of Playa Features	795	420	126
Average Playa Feature Basin Sizes & Ranges (ha)	3.35 (0.05-47.30)	2.22 (0.01-45.27)	2.25 (0.07-13.41)
# of Links	196,710	29,677	6,085
Coalescence Distance (km)	189.08	163.46	363.50
Graph Density	0.62	0.33	0.77
Average Node Connectance	2.08	3.31	1.63
Graph Diameter	9	12	6

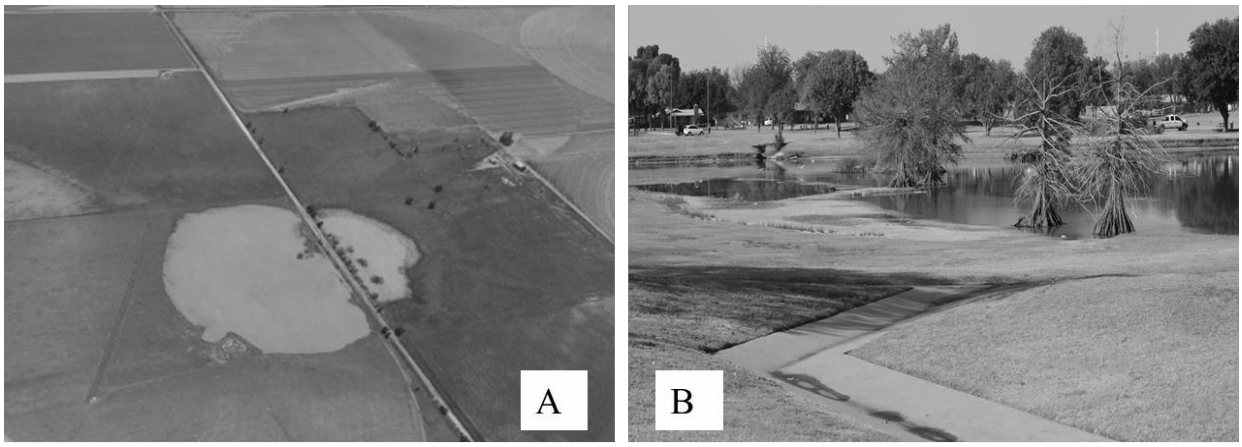

Figure 3.1. Examples of playas of the Great Plains of the United States. A) Playa with direct impervious surface alterations but not occurring within developed land use. B) Playa within developed land use but with only limited surrounding impervious surface. Photographs courtesy of the authors.

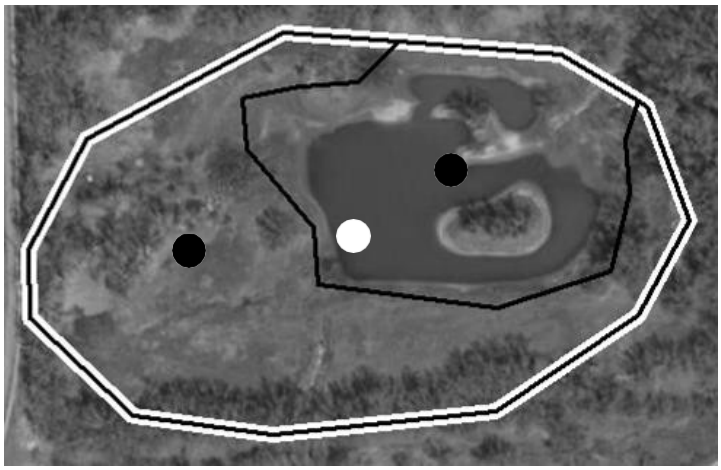

Figure 3.2. Example of Maps of Probable Playas classifications of playa wetlands consisting of two within-basin sub- features (black outlines, with centroids of each sub-feature symbolized by black circles). Alternatively, a playa basin may be depicted by the simple perimeter of the basin (white outline, with centroid of entire basin symbolized by a white circle).

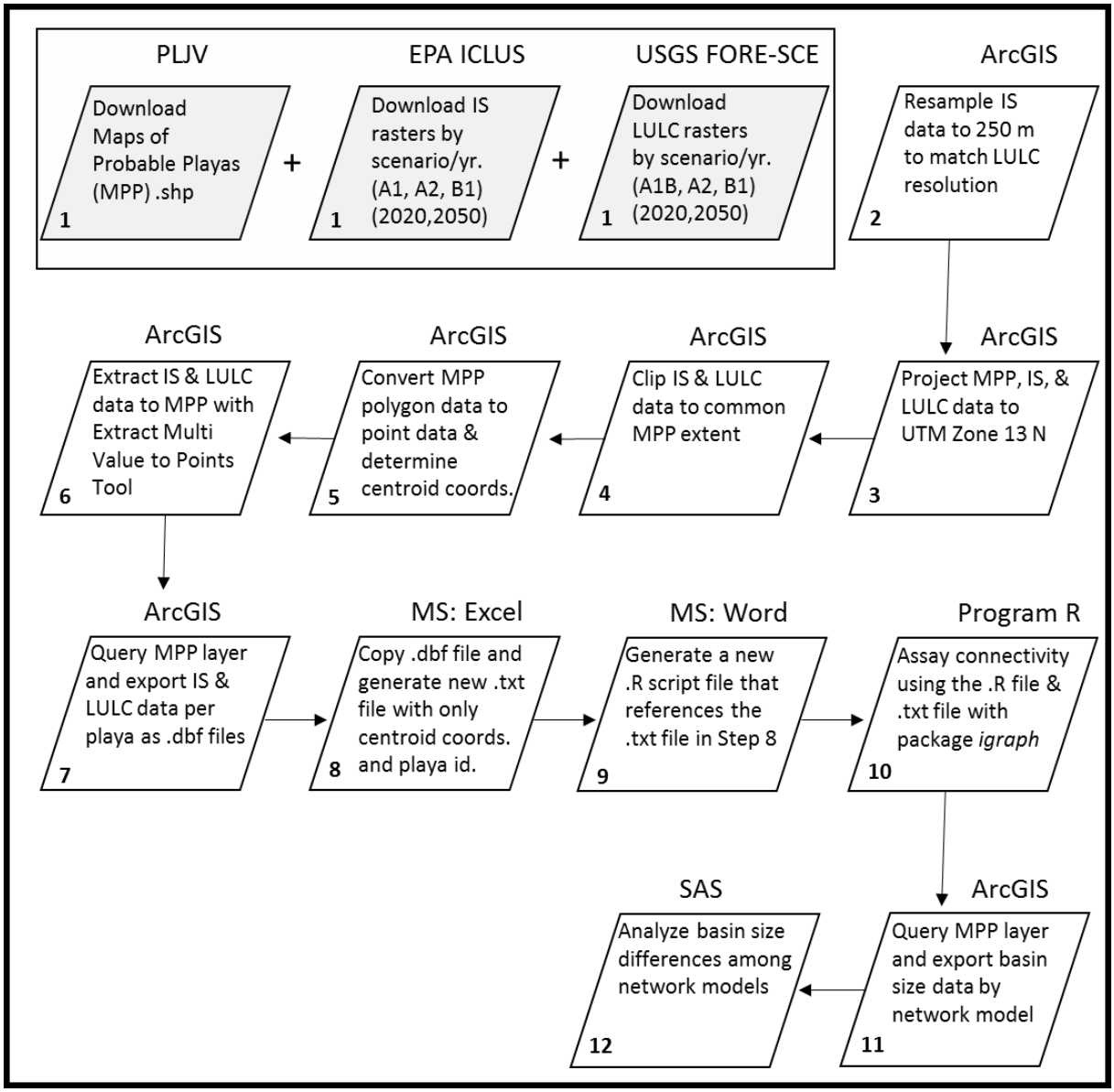

Figure 3.3. Schematic of data processing and general workflow.

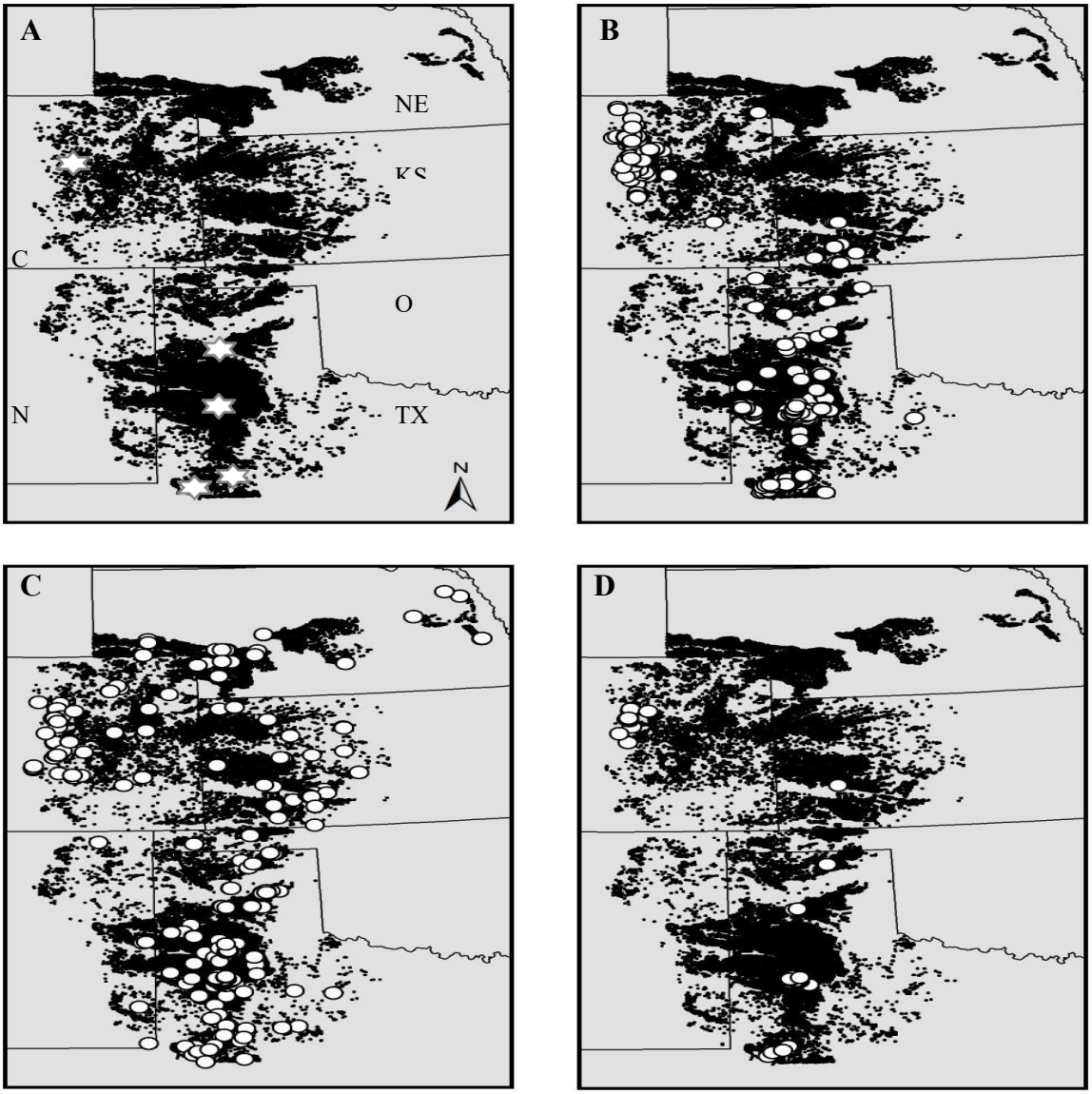

Figure 3.4. Extent and distribution of Great Plains playa features (black dots). A) Large metropolitan centers (white stars) of the region in 2020; from north to south: Denver, Amarillo, Lubbock, Midland, Odessa. B) Distribution of urban playas in 2050 (white circles) as identified by the ICLUS Model Network. C) Distribution of urban playas in 2050 (white circles) as identified by the FORE-SCE Model Network. D) Distribution of urban playas in 2050 (white circles) as identified by the Consensus Model Network.

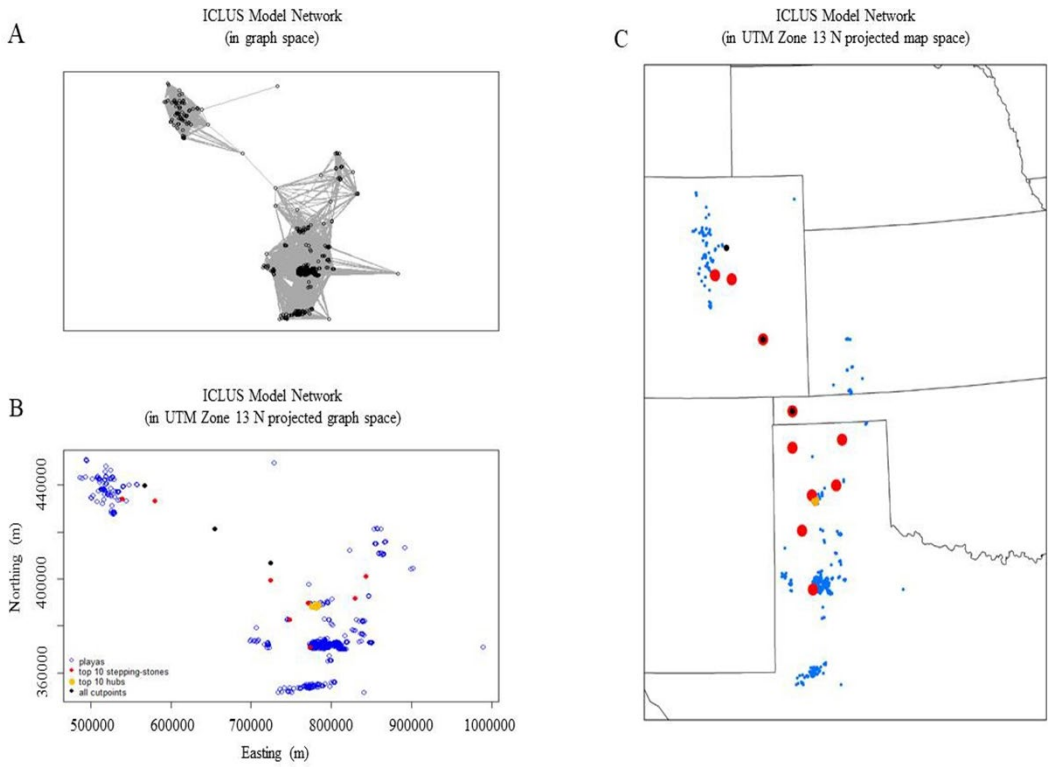

Figure 3.5. ICLUS Model Network connectivity: A) Top left image depicts linkages in unprojected graph space (gray lines) among playas (black rings). B) Bottom left image depicts locations of locations of playas (blue rings), top 10 stepping-stones (red circles), top 10 hubs (orange circles), and all three cutpoints (black circles) in UTM Zone 13 N projected graph space. C) Right image depicts the same information as in B, but is projected in UTM Zone 13 N projected map space. Note: due to icon overlap and close proximity (clustered in northern Texas), most hubs are not apparent.

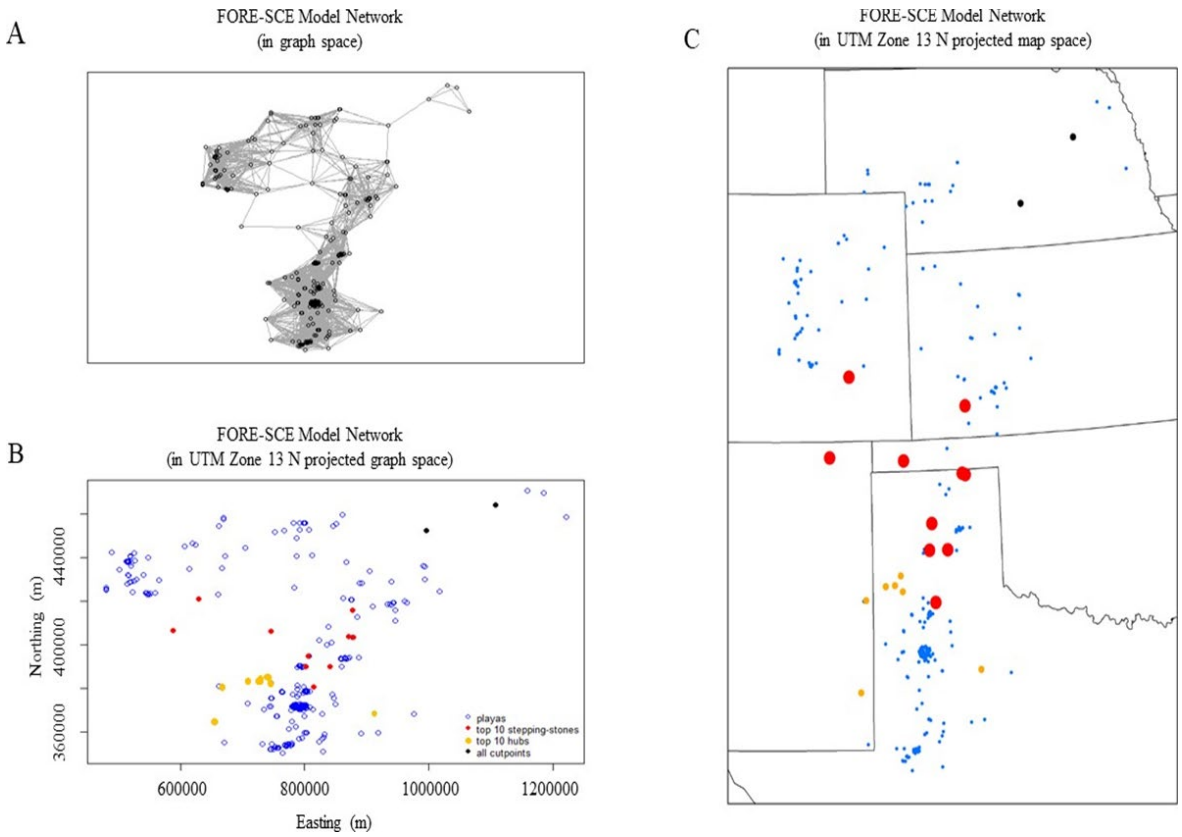

Figure 3.6. FORE-SCE Model Network connectivity: A) Top left image depicts linkages in unprojected graph space (gray lines) among playas (black rings). B) Bottom left image depicts locations of locations of playas (blue rings), top 10 stepping-stones (red circles), top 10 hubs (orange circles), and all three cutpoints (black circles) in UTM Zone 13 N projected graph space.
C) Right image depicts the same information as in B, but is projected in UTM Zone 13 N projected map space. Note: due to icon overlap and close proximity (clustered in northern Texas), some hubs are not apparent.

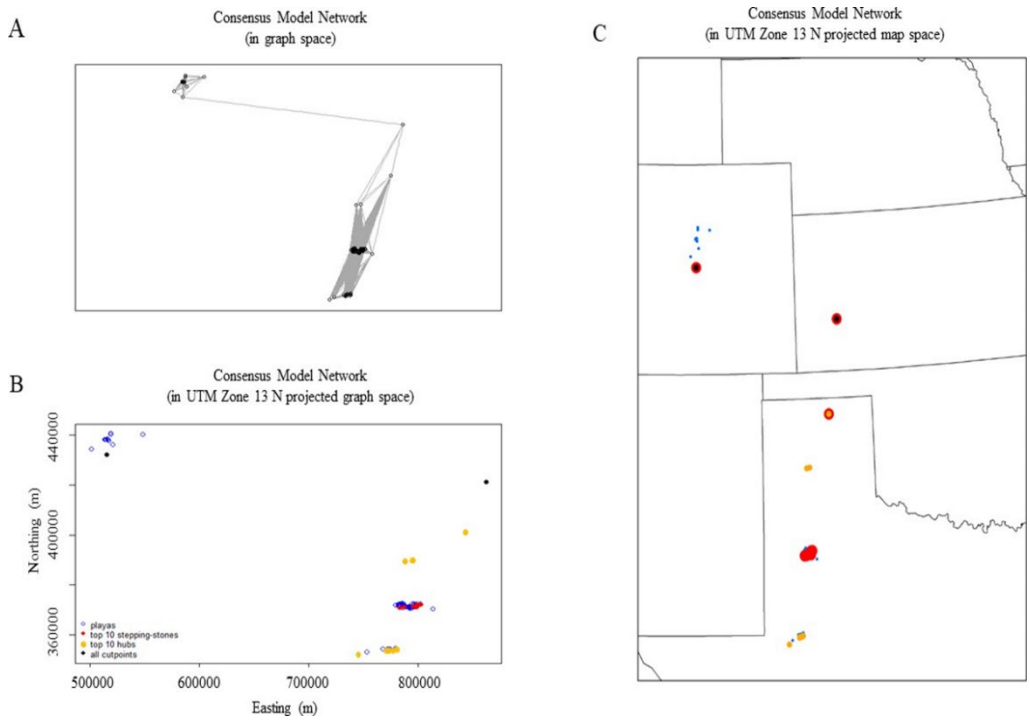

Figure 3.7. Consensus Model Network connectivity: A) Top left image depicts linkages in unprojected graph space (gray lines) among playas (black rings). B) Bottom left image depicts locations of locations of playas (blue rings), top 10 stepping-stones (red circles), top 10 hubs (orange circles), and all three cutpoints (black circles) in UTM Zone 13 N projected graph space. C) Right image depicts the same information as in B, but is projected in UTM Zone 13 N projected map space. Note: due to icon overlap and close proximity (clustered in northern Texas), some hubs are not apparent.

Supplementary Material. Summary of top 10 stepping stones, top 10 hubs, and all cutpoints with centroid coordinate information (UTM easting, northing) for each of the model networks. Note that playa sub-features may share the same basin identification code. Entries in *italics* are for playa basins that exist as top 10 stepping stones or top 10 hubs only when playa sub-features are ignored in connectivity analysis. Shading provided to better distinguish the model networks.

ICLUS Model Network			FORE-SCE Model Network			Consensus Model Network		
PPv4_ID	XUTM13	YUTM13	PPv4_ID	XUTM13	YUTM13	PPv4_ID	XUTM13	YUTM13
Top 10 Stepping-stones								
OK_499	724429.1	4068127.0	TX_20746	806370.7	3948983.0	TX_22019	843035.5	4011302.0
CO_1416	654285.6	4212626.0	TX_19122	840312.8	3902285.0	KS_21823	861937.9	4212569.0
TX_19159	770807.3	3898857.0	OK_229	745932.0	4061421.0	CO_1083	515016.2	4320918.0
CO_1784	579682.3	4333358.0	NM_2297	588114.7	4066625.0	TX_5983	802270.8	3721531.0
TX_21601	724295.9	3994410.0	CO_901	629633.9	4211190.0	TX_5330	798505.6	3713530.0
TX_16296	747586.1	3827647.0	TX_14292	815081.0	3807732.0	TX_5975	798881.1	3721270.0
CO_4169	539626.7	4341870.0	KS_16033	877167.2	4160205.0	TX_5957	799874.8	3721166.0
TX_19910	829138.9	3918701.0	TX_19173	801527.4	3900870.0	TX_5269	787291.3	3711801.0
TX_22016	843039.0	4011124.0	TX_22814	871105.1	4039365.0	TX_5444	795185.6	3714961.0
TX_5093	773255.8	3709201.0	TX_22719	878036.4	4036571.0	TX_5216	782785.7	3711050.0
			KS_7361	*783438.0*	*4262410.0*	*TX_5940*	*799538.0*	*3720760.0*
Top 10 Hubs								
TX_18674	775424.8	3886385.0	NM_541	666375.0	3811162.0	TX_22019	843035.5	4011302.0
TX_18674	775188.2	3886511.0	TX_17679	740440.3	3854846.0	TX_19076	795294.8	3897904.0
TX_18691	777905.0	3887351.0	TX_17675	740437.9	3854757.0	TX_19046	788059.6	3896260.0
TX_18729	782005.8	3888790.0	TX_16883	708337.4	3835914.0	TX_462	745380.5	3523302.0
TX_18710	779818.1	3888077.0	TX_16883	708292.6	3835820.0	TX_595	771098.7	3537520.0
TX_18685	780322.0	3887299.0	TX_16883	708430.5	3835868.0	TX_619	770554.8	3538570.0
TX_18685	780444.1	3887499.0	TX_16950	727755.0	3837812.0	TX_652	772286.3	3540056.0
TX_18685	780486.4	3887489.0	TX_3717	912159.1	3687761.0	TX_641	777148.4	3540075.0
TX_18583	780554.3	3883273.0	NM_1890	655619.2	3645661.0	TX_683	779642.1	3541665.0
TX_18759	782393.2	3889418.0	TX_16239	744780.6	3826759.0	TX_687	779249.1	3541976.0
TX_18559	*784822.0*	*3882080.0*	*TX_16197*	*745022.0*	*3825980.0*			
TX_18522	*777441.0*	*3880630.0*						
TX_18751	*781847.0*	*3889130.0*						
All Cutpoints								
CO_4915	567144.4	4396835.0	NE_21610	1107894.0	4641870.0	KS_21823	861937.9	4212569.0
CO_1416	654285.6	4212626.0	NE_3087	995820.8	4522880.0	CO_1083	515016.2	4320918.0
OK_499	724429.1	4068127.0						

CHAPTER IV

COMPARISON OF EUCLIDEAN, LEAST-COST PATH, AND LANDSCAPE RESISTANCE MODELLING IN ASSESSMENT OF PLAYA WETLAND CONNECTIVITY FOR AMPHIBIANS OF THE SOUTH-CENTRAL GREAT PLAINS (USA).

Introduction

Globally, amphibian diversity is in decline; causes vary, but two of the most prominent are climate change and land-cover alterations (Collins & Storfer, 2003; Hof, Araújo, Jetz, & Rahbek, 2011). For the amphibians of the south-central portion of the Great Plains of North America, aquatic habitat is concentrated at playas. Playas are intermittent, runoff-fed wetlands that are the only source of aboveground freshwater for large portions of the Great Plains, serving as hotspots of amphibian biodiversity within a terrestrial mosaic in a semi-arid climate (Venne, Tsai, Cox, Smith, & McMurry, 2012). Playa amphibians are subject to both climate change and land-cover alterations, especially as they co-relate to alterations in playa hydrology, making them at particular risk to these factors (Anderson, Haukos, & Anderson 1999; Gray, Smith, & Brenes, 2004; Gray, Smith, & Leyva, 2004). A decrease in habitat availability from climate change and/or land-cover change is expected to negatively affect populations directly as well as indirectly by impacting dispersal.

Dispersal is the underpinning of gene flow, habitat selection, and other fundamental biological processes. Anthropogenic landscape change that affects dispersal has thus been considered a key threat to biodiversity (Clobert, Baguette, Benton, & Bullock, 2012; Fahrig, 2003; Trakhtenbrot, Nathan, Perry, & Richardson, 2005; Travis et al., 2013). Dispersal through heterogeneous, arid landscapes (such as those of the south-

central Great Plains) would be particularly problematic for overland dispersers such as amphibians, which require aquatic breeding environments.

Consequently, their dispersal is influenced by aquatic habitat availability as well as by crossing terrestrial habitats to reach new aquatic habitats. Overland connectivity among playas should be highly dynamic due to the inherently dynamic nature of playa inundation from precipitation events (Bolen, Smith, & Schramm Jr., 1989; Smith, 2003; Wallace, Dauson, Bier, & Martin, 2014) as well as surrounding land-cover (Collins et al., 2014; Gray 2002; Gray et al., 2004a; Gray et al., 2004b; Ruiz et al., 2014). Within the south- central Great Plains, the landscape is primarily comprised of pasture/grassland, shrubland, and tilled croplands (Collins et al., 2014). With respect to crop type, the area is dominated by wheat, corn, cotton, soybeans, and sorghum. Soybeans are grown more extensively in northern portions of this area, whereas cotton, corn, wheat, and sorghum predominate in southern portions of the region (Collins et al., 2014). Based on studies conducted elsewhere on amphibians, crop type and habitat arrangement have been shown to influence dispersal (Cline & Hunter Jr., 2014; Cosentino, Schooley, & Phillips, 2011; Nowakowski, Veiman-Echeverria, Kurz, & Donnelly, 2015; Youngquist & Boone, 2014). Specifically, dispersal movements in agroecosystems are associated with closed canopy types (e.g. from tall grasses or in forested areas) that reduce the risk of desiccation but may incur other risks (Cline & Hunter Jr., 2014; Cosentino et al., 2011; Gray et al., 2004a; Nowakowski et al., 2015; Youngquist & Boone, 2014). Indeed, research by Consentio et al. (2011) has documented that soybeans may facilitate movements of amphibians in agroecosystems located in Illinois, USA. However, these results were not

consistent with those by Collins & Fahrig (2017) for agroecosystems containing soybeans in eastern Ontario, Canada. Each of these studies provided a rare and explicit delineation of crop type influences on amphibian movements for soybeans; thus, we also specifically addressed the effect of soybeans in our study.

Despite the importance of both aquatic habitat availability and land use on amphibian dispersal, few studies have described amphibian dispersal patterns within the south-central Great Plains (Gray, 2002; Gray et al., 2004a; Gray et al., 2004b). Those that have were limited to a relatively small number of playa wetlands (16), examined only a limited time scale of dispersal, and did not examine effects of different crop types on dispersal. However, these studies can serve as a basis by which to develop a regional model of dispersal for the playa amphibian community. Our study incorporates these initial findings and builds from more recent literature documenting that playa hydrology is affected by crop type in the surrounding watershed (Collins et al., 2014). The examination of animal dispersal in heterogeneous and dynamic landscapes has focused on quantifying landscape connectivity. These can be grouped into two "families" of techniques that quantify different aspects of connectivity. Structural connectivity consists of how the spatial configuration of the landscape impedes or facilitates movement and is quantified in terms of spatial properties such as density and proximity of habitat patches; in contrast, functional connectivity is a measure of how an organism actively responds to landscape structure and so is quantified in terms of actual movement pathway location and properties such as length and tortuosity (Tischendorf & Fahrig, 2000). As such, structural connectivity is effectively quantified by use of graph theory, whereas functional connectivity is

typically quantified by techniques based on electrical circuit (resistance) theory. Graph (or network) theory was developed to investigate pairwise relationships between objects within networks ("graphs"). In graph theory, a network is constructed from nodes (i.e., playas) that are connected by edges (i.e., dispersal routes). For in-depth discussion of graph theory, see Bondy & Murty (1976) and West (1996). A graph's topology (density and arrangement of nodes) can be quantified by a number of metrics, with perhaps the most ecologically crucial one being the coalescence distance: this is the distance that an organism must be capable of traveling to disperse through the network, moving from node to node (Ruiz et al., 2014). This distance is effectively the farthest distance between nearest-neighbor pairs of nodes. If this distance is greater than the maximum known dispersal distance for a given species, then the network is considered to be fragmented into isolated clusters of nodes. If, however, this distance is within the dispersal capacity of a species, then the entire network can be considered a single potential population unit. Because this critical threshold distance hinges upon graph topology, its value changes with changing number and arrangement of nodes. For the playa network, topology is a highly dynamic character (due to the intermittent nature of playa inundation) that is typically beyond the dispersal capacity of most terrestrial organisms (Ruiz et al., 2014), but the network can also be examined at distances smaller than the coalescence distance, such as distances that are more appropriate dispersal distances for amphibians. At these smaller distances, nodes within that distance form habitat clusters: groups of playas that are within dispersal range of an amphibian. Identifying the number and density of such habitat clusters is an important feature in quantifying

structural connectivity for management of amphibians in arid environments (Drake, Griffis-Kyle, & McIntyre, 2017a; Drake, Griffis-Kyle, & McIntyre, 2017b; McIntyre, Drake, & Griffis-Kyle, 2016).

Additionally, an individual node may play an outsized role in supporting connectivity among habitat patches; three of the most important and commonly used roles are as a cutpoint, hub, or stepping-stone, based on the number and orientations of connections (linkages to other nodes) within the network (Ruiz et al., 2014). A cutpoint is a node that if removed from the network results in a disproportionally high degree of network fragmentation (i.e., disruption of dispersal through the network, with dispersal instead only occurring at more localized scales within nearby clusters of nodes). Hubs are those nodes that are connected to more nodes relative to other nodes within the network (Minor & Urban, 2008). Finally, a stepping-stone is a node that facilitates energetically efficient dispersal through the network due to its strategic location along the shortest path through the network.

Graph theory applications for investigation of dispersal in heterogeneous landscapes were developed in the early 1990s, with significant advancement in these applications by the early 2000s (Bunn, Urban, & Keitt, 2000; Cantwell & Forman, 1993; Moilanen, 2011; Urban & Keitt, 2001; Urban, Minor, Treml, & Schick, 2009). The strengths of graph theory include its straightforward approach that does not rely upon demographic data that may not exist for a species in a given area (Minor & Urban, 2007). In addition, unlike other connectivity approaches, graph theory permits quantification of the connectivity roles of individual nodes.

These features make graph theory approaches ideal for rapid conservation

assessments and prioritization of individual habitat patches (Minor & Urban, 2007) and is an active avenue of connectivity studies (Kool, Moilanen, & Treml, 2013). However, there are limitations to graph-centric assessments of landscape connectivity (Moilanen, 2011). For example, there are numerous ways of assigning roles to individual nodes (such as those of cutpoint, stepping-stone, or hub, among others) or otherwise quantifying connectivity via metrics (Pascual-Hortal & Saura 2006; Rayfield, Fortin, & Fall, 2011). More broadly, graph theory can only infer immigration and emigration and neglects birth and death rates that influence patterns of persistence or extinction risk across landscapes. Furthermore, graph theory approaches use Euclidian (straight-line) distances to represent linkages among nodes, with output that is effectively a null model but likely not a realistic representation of movements by terrestrial, non-volant (overland) dispersers through a network. And perhaps most importantly, graph theory ignores the influences of the intervening landscape matrix that separates nodes. These limitations can make integration of graph theory-based recommendations into conservation planning problematic (Bergsten & Zetterberg, 2013; Zetterberg, Mörtberg, & Balfors, 2010).

In contrast to the graph theory family of (structural) connectivity approaches, electric circuit theory has been used to develop two alternative ways of examining (functional) connectivity by explicitly examining the influence of the intervening landscape matrix by assigning “costs” or resistances to movement to the different environmental features of the matrix, such as land use/land cover, slope, or elevation. The first-developed of these approaches, least cost path (LCP) modeling, is a

mathematical calculation that determines the shortest path distance between a source and target node, typically using Dijkstra's algorithm (Dijkstra, 1959) or a derivative. LCP modeling is often accomplished in a GIS-based environment, using raster data layers to identify a single path (one raster cell wide) that represents the least-accumulated cost possible between points (Adriaensen et al., 2003; Bunn et al., 2000). For example, LCP can be used to find the single least cost path that water would take through a landscape by assigning higher costs to higher elevations than to lower ones, which would accurately depict water flowing downhill. Although LCP modeling of dispersal is relatively inexpensive and easily programmable, results are influenced by raster data development (for examples using artificially generated landscapes, see Rayfield, Fortin, & Fall, 2010) and lack of a biological foundation for cost assignments to environmental features (Sawyer, Epps, & Brashares, 2011; Zeller, McGarigal, & Whiteley, 2012). Moreover, LCP modeling of dispersal along single movement pathways may represent an overly simplistic abstraction of real-world dispersal (Fahrig, 2007; Pinto & Keitt, 2009; Pullinger & Johnson, 2010).

Both graph-centric and LCP modeling techniques may thus suffer from an inability to accurately portray the complexity of animal movements through heterogeneous and dynamic landscapes. In contrast, another form of modeling derived from electrical circuit theory uses resistance costs of each environmental layer category (like in LCP modeling) but does so in such a way that generates multiple paths through the network along a gradient of costs rather than trying to resolve to a single path solution as in LCP modeling (McRae, 2006; McRae & Beier, 2007; McRae,

Dickson, Keitt, & Shah, 2008). As a result, this landscape resistance to movement (LRM) modeling has the capacity to overcome the other methods' shortcomings by identifying multiple potential corridors and regions of dispersal bottlenecks. LRM modeling is not without its own drawbacks, being the most "data hungry" and computationally intensive of the three approaches (Spear, Balkenhol, Fortin, McRae, & Scribner, 2010; Nowakowski et al., 2015; Zeller et al., 2012). Furthermore, a key component of LRM is subjective, which is how to assign resistance values (via presence/absence data, historical distribution data, or personal opinions; Spear et al., 2010; Nowakowski et al., 2015; Zeller et al., 2012), and there have been relatively few examinations of model sensitivity and assumptions of animal movement and selection decisions (Zeller et al., 2012). Nevertheless, LRMs have provided valuable insights toward a comprehensive understanding of functional connectivity (Cushman, Landguth, & Flather, 2013; Mazerolle & Desrochers 2005; Nowakowski et al 2015, Pittman, Osbourn, & Semlitsch, 2014; Spear, Cushman, & McRae, 2015; Wade, McKelvey, & Schwartz, 2015; Youngquist & Boone, 2014). Indeed, landscape resistance models have been used to explore dispersal patterns and gene flow in several taxa for conservation and management planning, and they are particularly apropos for examining amphibian dispersal because it is readily recognized that the permeability of terrestrial habitats should influence overland dispersers that are sensitive to desiccation, with certain land-cover types being likely to promote and others to inhibit amphibian movements (Wade et al., 2015; Zeller et al. 2012).

Most LRM-based studies of amphibian movement have been on forest species, with higher resistance values for agricultural and urbanized areas. Although some

applications of LRMs for arid-land amphibians exist (Bishop-Taylor, Tulbure, & Broich, 2015; Drake et al., 2017a; Mims, Phillipsen, Lytle, Kirk, & Olden, 2015; Pilliod, Arkly, Robertson, Murphy, & Frank, 2015), these studies were limited in scope of species investigated, dominated by riverine connectivity of habitats, or represented environments with extensive elevational gradients. Grassland ecosystems have received relatively little scientific attention with respect to LRMs of amphibian dispersal. These regions are non-forested, agriculturally dominated, and subject to extensive periodic droughts; thus, connectivity among the ephemeral wetlands of these regions is of conservation importance (Cushman et al., 2013; Johnson et al., 2010; McIntyre et al., 2014; Uden, Hellman, Angeler, & Allen, 2014; Uden et al., 2015). These anthropogenically modified arid regions represent a new area in which LRM research can be applied, especially as it relates to amphibians, which are intimately influenced by limited aquatic habitat availability. Our research addresses calls for more landscape connectivity studies in urban areas, on non-charismatic species, and landscapes outside forested areas (LaPoint, Balkenhol, Hale, Sadler, & van der Ree, 2015; Correa Ayram, Mendoza, Etter, & Salicrup, 2016). No single technique can completely encapsulate landscape connectivity for all regions or species (Calabrese & Fagan, 2004; Tischendorf & Fahrig, 2000). The strengths of graph theory lie in its simplicity (not requiring demographic data) and its unique ability to identify the contributions of individual nodes for management. Being based solely on distance between nodes and ignoring intervening landscape structure, however, graph theory may be relatively unrealistic for many taxa and thus provides a null model of landscape connectivity. Landscape resistance models, in

contrast, are more realistic in providing multiple possible dispersal paths through a heterogeneous environment, but they are also much more data-intensive. Least-cost paths are intermediate between these other methods. Thus, these three methods—graph theory, least-cost paths, and landscape resistance models—are complementary ways of examining structural and functional landscape connectivity, at the level of individual nodes as well as at the path level. Because the core aim of our study is to provide a comprehensive understanding of landscape connectivity for amphibian dispersal within the south-central Great Plains, we incorporated all three approaches.

Methods

Data

Our focal region was based on the playa wetlands contained within the playa clusters (PC) database developed by the Playa Lakes Joint Venture (https://pljv.org/for-habitat-partners/maps- and-data/playa-decision-support-system/texas-playa-decision-support-tools/, accessed September 2017). This database mapped 904 playa wetland clusters across ~68 million hectares of the Great Plains in Colorado, Kansas, Nebraska, New Mexico, Oklahoma, and Texas (Fig. 4.1). These playa clusters are areas with high playa density or high playa surface area within a 2 km radius (McLachlan, Daniels, & Bartusevige, 2014).

Although the PC was developed with a focus on bird conservation (McLachlan et al., 2014), the 2 km threshold distance is within the estimated dispersal ranges for a majority (9) of the 13 amphibian species that occur within the south-central Great Plains (AmphibiaWeb, 2014; Anderson et al., 1999; Gillis, 1975; Gray et al., 2004a;

Gray et al., 2004b; Griffis-Kyle, Kyle, & Jungels, 2011; Kenney & Stearns, 2015; Lannoo, 2005; Mayhew, 1965; NatureServe, 2014; Ramesh, Kyle, Perry, & Farmer, 2012; Table 4.1). Of these species, *Spea multiplicata*, *Spea bombifrons*, *Anaxyrus cognatus*, and *Ambystroma tigrinum mavortium* are the most abundant and widespread in this region (Gray et al., 2004a; Gray et al., 2004b).

For some species-specific dispersal data, Table 4.1 may only represent adult movements, a key consideration for some amphibians, as larger-scale dispersal events may occur mainly during juvenile (metamorph) stages (Cushman, 2006; Semlitsch, 2008; Spear et al., 2010, Pittman et al., 2014; Smith & Green, 2015). Additionally, it is important to note that outside of the work by Gray et al. (2004a and 2004b) and Griffis-Kyle et al. (2011), species-specific estimates of maximum dispersal ability are not available specifically for the south-central Great Plains. However, the maximum dispersal distance of several species that occur in this region has been estimated at less than 1 km in non-shortgrass prairie areas. Some species, however, notably the American Bullfrog, may have dispersal ranges upward of several kilometers. (Indeed, it should be noted that the American Bullfrog may be considered invasive to some portions of the region and poses significant threats in other aquatic systems in the United States and internationally; Ficetola, Thuiller, & Miaud, 2007). Thus, the estimated maximum dispersal distances in Table 4.1 ought to be considered as a conservative means of estimating overall playa amphibian movement capabilities.

From these limited amphibian dispersal data, we categorized each of the 13 species into one of four groups based on their estimated maximum adult dispersal ability

(Table 4.2). We subsequently used these thresholds in conjunction with PC features to delineate distinct habitat patches for each group. Additionally, we delineated habitat patches at the 15 km dispersal threshold distance (roughly twice the length of the maximum dispersal distance of the American Bullfrog), to model anecdotal reports of extreme amphibian dispersal events. This approach allowed us to model both structural and functional connectivity of playa amphibians for the period 2008 to 2016. This focal timeframe was a direct consequence of land-use/land-cover data availability as described in the following paragraph.

To examine regional land-use/land-cover change during our focal timespan, we used the United States Department of Agriculture's National Agricultural Statistics Service online Cropscape- Cropland Data Layer (CDL) (https://nassgeodata.gmu.edu/CropScape/, accessed September 2017). The CDL contains nationwide annual coverage estimates of >250 categories of agricultural and land-use/land-cover data at a 30 m spatial (raster) resolution and have been used in other studies within the playa region (Collins et al., 2014; Ruiz et al., 2014). However, data for the entire PC region were only available from 2008 to 2016 at the start of our project; thus, our focal timespan coincides with these years.

As amphibian movement and dispersal may be influenced by local soil moisture levels, which influence desiccation risk (Cosentino et al., 2011; Mazerolle & Desrochers, 2005; Nowakowski et al., 2015), we also incorporated the potential effects of irrigation on amphibian dispersal within the playa region. Irrigation practices (primarily center-pivot systems) within the playa region are often highly dependent upon access to the Ogallala (High Plains) Aquifer and may fluctuate in

intensity throughout the growing season and from year to year in response to local precipitation patterns, crop rotations, and landowner activities (Heintzman, Starr, Mulligan, Barbato & McIntyre, 2017). We used the Moderate Resolution Spectroradiometer (MODIS) Irrigated Agriculture Dataset for the United States (MIrAD-US) from the USGS US Irrigation Early Warning and Environmental Program (https://earlywarning.usgs.gov/USirrigation, accessed October 2017). These datasets were developed to map irrigation practices at 250 m and 1 km (which we used) resolutions across the conterminous United States via MODIS satellite imagery, USDA Census of Agriculture irrigated area statistics, and National Land Cover Dataset (NLCD) information. For more details, see Brown & Perves (2014), Brown, Pervez, & Maxwell (2009), and Perves & Brown (2010). MIrAD-US data are available from 2002, 2007, and 2012; thus, we included data from 2007 and 2012 in our analysis, as these years immediately preceded or occurred during our focal time span. Furthermore, to more accurately represent land-use/land-cover change during our focal timespan, we paired CDL data from 2008-2011 with 2007 MIrAD-US data and similarly paired CDL data from 2012-2016 with 2012 MIrAD-US data.

Data Processing and Model Development

We used a modelling approach developed in ArcGIS 10.6 (Esri, Redlands, CA) to examine structural and functional connectivity of amphibians within the playa region during our focal timespan. We began by first projecting the PC, MIrAD-US, and CDL layers into UTM Zone 13 N via the Project and Project Raster Tools in ArcGIS 10.6.

Next, we used the Minimum Bounding Geometry Tool and the PC layer to develop a temporary, rectangular vector layer. This new temporary layer was then used with the Buffer Tool to develop a 10 km buffer around the temporary layer. This buffered layer then served as our final study extent, which facilitated a standardized data processing size for all focal years, allowed for easier incorporation of raster data for analysis, and encapsulated all potential amphibians movements among playas (because this distance was ~3 km wider than the maximum known dispersal distance of American Bullfrog).

Using a digital copy of the projected UTM Zone 13 N PC layer, we used the Calculate Geometry Tool in ArcGIS 10.6 to calculate the x-coordinate and y-coordinate locations of the centroid for each of the 904 playa wetland clusters found in the PC. The *igraph* package (Csardi & Nepusz, 2006) in R 3.5.3 (R Development Core Team, 2019) was used to determine the coalescence distance to the nearest meter. Following identification of coalescence, we then identified nodes as hubs, cutpoints, or stepping-stones. Additionally, we assessed the global-scale structural connectivity metrics of graph density (ratio of links present to the number of all possible links among nodes), average nodal connectance (number of connections that a node has with other nodes at coalescence, with higher values indicative of greater path redundancy), and graph diameter (the number of links forming the longest path through the network) to holistically describe network topology (Drake et al., 2017a; Drake et al., 2017b; Heintzman & McIntyre, 2019; McIntyre, Collins, Heintzman, Starr, & van Gestel, 2018; Ruiz et al., 2014).

For assessments of regional functional connectivity, we developed three unique

models for our focal region: Soybeans Best Model (SBM), Cropland Combined Model (CCM), and Natural Lands Model (NLM). These models were based on land-use/land-cover change with an emphasis on agricultural categories (from the CDL), as well as irrigation (from MIrAD-US) across the focal region. To develop these models, we first considered the data constraints of the CDL. The CDL has >250 land-use/land-cover categories, yet not all crop types are present in all years in the south-central Great Plains. Therefore, we reclassified these categories to 14, following the protocols in Collins et al. (2014). Additionally, we documented that CDL layers from 2008 and 2009 were only available at 56 m resolution whereas layers from the other years were at 30 m resolution. For data consistency, we therefore resampled each of the CDL layers to 840 m resolution. The result of these steps ensured that each of the CDL layers from 2008-2016 consisted of the same 14 land-use/land-cover classes and was composed of the same number of pixels, necessary to develop resistance surface layers for LRM in later steps (Table 4.3). The MIrAD-US layers required conversion of unclassified, 32-bit unsigned floating-point raster data into classified, 8-bit unsigned integer raster data via the Export Raster Data function. This procedure resulted in a 17-class category index of irrigation that was consistent across the SBM, CCM, and NLM models (Table 4.3).

Although development of resistance surfaces is necessary to model functional connectivity via LRM, deriving resistance values for individual species or groups of species, e.g. amphibians, is a subjective process (Cushman, 2006; Nowakowski et al., 2015; Spear et al., 2010; Zeller et al., 2012), with no consensus as to which layers, data types, or numerical scaling should be used (Zeller et al., 2012). For our study,

we informed development of our resistance surfaces from empirical studies of amphibian dispersal among different land-use/land-cover types (Cline & Hunter Jr., 2014; Cosentino et al., 2011; Collins et al., 2014; Gray, 2002; Gray et al., 2004a; Gray et al., 2004b; Nowakowski et al., 2015; Youngquist & Boone, 2014). Using Circuitscape 4.0 and the Circuitscape ArcGIS toolbox (McRae, Shah, & Mohapatra, 2013) paired with the Gnarly Landscape Utilities (McRae, Shirk, & Platt, 2013; Shirk & McRae, 2013) and Linkage Mapper ArcGIS toolbox extensions (McRae & Kavanaugh, 2011), we developed a base case of resistance values (using the sum operator in Gnarly Landscape Utilities to additively account for both land-use/land-cover resistance and irrigation status resistance) for each of our three models (SBM , CCM, NLM). These base cases were then used to develop individual resistance surfaces for each year from 2008-2016. For three land-use/land-cover categories (wetland, open water, and developed), we used the Cell Expansion function to simulate soft edge effects (wetland and open water) and hard edge effects (developed) for potential amphibian dispersal for each case across all focal years. The resistance surface parameterization (Tables 4.4-4.9: 2008 and 2016 are provided as examples), shows the individualized resistance values used in each of the base cases.

Beginning with the SBM base case, we assigned resistance values of land-use/land-cover types based on results from Costentino et al. (2011), who had specifically identified soybeans as having lower resistance to amphibian movement compared to corn. Thus, we considered soybeans [resistance value = 7] as the least resistive of the five-primary regional crop-type classes. We then used a first-principles approach (where developed [25] and barren [27] areas were deemed likely to be highly

resistive to movement of amphibians; open water [5] and wetlands [1] were considered less resistive to movement of amphibians), coupled with photographic assays of crop fields, to infer canopy structure and, thus, resistance of the remaining four primary crop type classes at maturity (corn [19], cotton [11], sorghum [13], wheat [15]). For the double crops CDL category, we assigned a resistance value slightly higher than the average resistance value of the five primary regional crop types [17], as planting/harvest schedules likely varied. The "other" crop category was assigned a value slightly higher than the average between developed and double crops categories [23]. Since regional amphibians are associated with playas in grassland and pasture-like settings (Gray et al., 2002; Gray et al., 2004a; Gray et al., 2004b) we assigned a resistance value for grass/pasture lower than that of soybeans [3]. Lastly, we considered the forest category as slightly more resistive than soybeans, given their regional rarity [9], with shrublands more resistive than corn but not as resistive as developed [21]. Resistance value assignments for land-use/land-cover categories of the CCM and NLM were identical to the SBM, with two exceptions: the cropland category [15] was slightly higher than average of each of the five-primary regional crop-type classes, and the natural lands category [3], based on the supposition that shrubland and grass/pasture categories could act to facilitate amphibian dispersal due to their relatively limited anthropogenic alterations. Resistance value assignments for irrigation status used a binary irrigated [0] or non-irrigated [1] classification scheme, based on index values derived from MIrAD-US data. For the SBM and CCM, all index values $\geq$25 were assigned as [0], while those <25 were assigned as [1]. For the NLM, all index values $\geq$6 were assigned [0], while

those <6 were assigned [1]. For each of the SBM, CCM, and NLM models, the possible resistance values ranged from 1-30, akin to the range of resistance values used by Drake et al. (2017). Considering that our study is the first to assign resistance values for amphibian dispersal in the south-central Great Plains, with no consensus exists for how to assign resistance values (Zeller et al., 2012), and given the dynamics of playa hydrology (Collins et al., 2014; Ruiz et al., 2014; Starr et al., 2016), we feel our base case resistance surfaces are logical representatives of regional amphibian dispersal potentials. Relatedly, we acknowledge that our use of PC data assumed that the clusters themselves and the playas contained within a cluster, were suitable habitat (i.e. inundated) for amphibians. This assumption is likely extremely unlikely to occur (Collins et al., 2014; Ruiz et al., 2014; Starr et al., 2016), yet was necessary to incorporate due to computational limitations and a lack of existing data on playa inundation patterns across the entirety of the playa region during our focal timespan.

For each of the SBM, CCM, and NLM models, we analyzed connectivity using protocols adapted from Drake et al. (2017a). We examined least cost paths (LCPs) as identified via the Circuitscape ArcGIS toolbox, with the LCPs spatially limited to a single pixel in width (the same grain as the input data layers). Because we were interested in long-term changes in potential LCP locations in our focal area, we merged LCPs across years for each model. From this merged layer, we used the Line Density, Round Up, and Reclassify tools in ArcGIS to better approximate and visualize LCP overlap across space in a binary raster form (path locations vs. non-path locations). We then used a binary true/false logic test via the Combine Tool in

ArcGIS to quantify the presence of LCP overlap among models.

Because results from LRMs (and subsequently derived LCPs locations) are influenced by input resistance values (Zeller et al., 2012), we performed a sensitivity analysis of the effects of altering our initial resistance values. We assessed differences in modelled LCP locations by reducing our CDL resistance values by increments of five (Minus 5 Case) or, conversely, increasing them by five (Plus 5 Case), and then rerunning our procedure as outlined above. This process assessed changes in magnitude, but not the relative directions of resistances. For example, the developed category was still more resistant than individual crops. To avoid processing errors due to zero or negative values of resistance, we truncated those values to 1 (Tables 4.4-4.9). We assessed sensitivity for two dates (2008 - start of focal timescale, and 2016 - end of focal timescale) for each of the three base case models (SBM, CCM, and NLM). Our decision to bracket resistance values by either -5 or +5 to assess sensitivity followed the approaches of Beier, Majka, & Newell (2009) and Drake et al. (2017), who assessed the effects of uncertainty when modelling connectivity in other arid environments. As discussed by Zeller et al. (2012), no consensus exists for how to develop or parameterize connectivity landscape resistance models. Thus, we feel by addressing uncertainty in our modelled sensitivity resistance surfaces that we further enhanced our representation of regional amphibian dispersal potentials.

Results

Structural Connectivity

Coalescence of the 904 playa wetland clusters of the south-central Great Plains was achieved at 92.71 km and consisted of 25,694 linkages among the nodes (playa clusters). Graph density was 0.06, with an average nodal connectance of 5.39 and a graph diameter of 1,563.5 km. The locations of the 10 top-ranked stepping-stones, hubs, and all three cutpoints (Drake et al., 2017a; Drake et al., 2017b; Heintzman & McIntyre, 2019; McIntyre et al., 2016; Ruiz et al., 2014) are shown in Fig. 4.2. At the 15 km dispersal threshold, there were 435 sub-networks identified, which further underscores the challenges faced by regional dispersing amphibians, since most of these sub-networks exist in relative isolation, beyond the dispersal range of most species (Fig. 4.3).

Functional Connectivity

Soybeans Best Base Case Model

LRM output for the SBM base case from 2008-2016 (Fig. 4.4) indicates changes in projected resistance for potential dispersal of non-volant organisms (i.e., amphibians) among playa wetland clusters. These differences were most pronounced along the eastern portions of the network. In the southern portions of the playa region, there were marked differences in the size and distribution of high-resistance regions. The subsequently derived LCP network for the SBM base case (blue lines of Fig. 4.5) also highlight the differences in modelled potential movement pathways through space and time.

Cropland Combined Base Case Model

LRM output for the CCM base case from 2008-2016 (Fig. 4.6) also indicate dynamic changes in projected resistance; however, this case features a comparatively less-resistive eastern border compared to the SBM. This model depicts several high-resistance areas in southern portions of the playa region, as does the SBM. The LCP network derived for the CCM base case (yellow lines of Fig. 4.7) also reflect the very dynamic southern portions of the focal region.

Natural Lands Base Case Model

The NLM base case from 2008-2016 has much less resistance when compared to the SBM and CCM (Fig. 4.8). The NLM features extensive low-resistance areas in the western portions of the playa region. Many of these observed patterns are attributed to the presence of pasture/grassland and shrubland. The LCP network derived from the NLM (red lines of Fig. 4.9) includes several near-Euclidian connections among playa clusters through these areas of low resistance.

Variation by Year within Model

The locations of LCPs varied throughout our focal timespan, depending on model (Figs. 4.5, 4.7, 4.9), but there were several areas of congruence. Indeed, some LCP locations across years within a base case completely overlapped (Fig. 4.10).

Congruence across Models

We quantified the amount of overlap of LCPs across the three base models during our focal timespan (Fig. 4.11). The results indicated that 57% of LCPs overlapped among all base case models, with 24% of LCPs overlapping with at least one other base case model.

Sensitivity Analysis Results

Overall, the sensitivity analyses indicated that our LCPs locations were sensitive to the changes in the magnitude of resistance value assignments.

SBM for 2008 and 2016

The resistance surfaces (Fig. 4.12) and corresponding LCP locations (Fig. 4.13) of the SBM model for 2008 show the projected changes in potential movement pathways through the playa region due to our modifications of resistance values. For illustrative purposes of LCP overlap, we denoted Minus 5 case LCPs in blue, Base Case LCPs in yellow, and Plus 5 Case LCPs in red, and then used color logic to identify areas of overlap (Fig. 4.14). This color scheme is exclusive to results from the sensitivity analysis are not equivalent to those in the previous section or figures. We found that 45% of LCPs overlapped among the Minus 5, Base, and Plus 5 cases, and 23% of the remaining LCPs overlapped with at least one other layer used in the sensitivity analysis (green lines [Minus 5 Case and Base Case LCP overlap], orange lines [Base Case and Plus 5 Case LCP overlap], and purple lines [Minus 5 Case and Plus 5 Case LCP overlap]) (Fig. 4.14).

The resistance surfaces (Fig. 4.15) and corresponding LCPs (Fig. 4.16, shaded in blue as described above) of the SBM for 2016 show the projected changes in

potential movement pathways through the playa region due to our modifications of resistance values. For 2016, 46% of LCP locations overlapped among the Minus 5, Base, and Plus 5 cases, and 23% of the remaining LCPs overlapped with at least one other model (Fig. 4.17).

CCM for 2008 and 2016

The resistance surfaces (Fig. 4.18) and corresponding LCPs (Fig. 4.19) of the CCM model for 2008 show the projected changes in potential movement pathways through the playa region due to our modifications of resistance values. LCPs locations overlapped 45% among each of the Minus 5, Base, and Plus 5 cases, and 22% of LCPs locations overlapped with at least one other layer used in the analysis (Fig. 4.20). Resistance surfaces (Fig. 4.21) and LCP locations (Fig. 4.22) for 2016 also indicate changes in potential movement pathways through the playa region based on our assigned relative resistance values. We documented that 47% of LCP locations overlapped among each of the Minus 5, Base, and Plus 5 cases. An additional 23% of LCPs locations overlapped with at least one other model (Fig. 4.23).

NLM for 2008 and 2016

NLM resistance surfaces (Fig. 4.24) and LCPs (Fig. 4.25) of the NLM sensitivity analysis for 2008 show that LCPs locations overlapped 44% overall, with an additional 23% of LCPs overlapping with at least one other model (Fig. 4.26). Similarly, resistance surfaces (Fig. 4.27) and corresponding LCPs (Fig. 4.28) for 2016 exhibited 44% overlap, and 23% overlapped with at least one other case (Fig. 4.29).

Discussion

Our analyses of recent land-use/land-cover structural connectivity changes for the span 2008-2016 and the subsequent effects on modelled functional connectivity among playa wetland clusters for amphibians of the south-central Great Plains indicate a relatively high degree of potential network overlap for dispersal when bases cases (SBM, CCM, and NLM) are considered (57% among base cases models and an additional 24% between at least two base case models; 81% overall). This overlap through time, across models, and with respect to changes in resistance values suggest that the playa wetland network features potentially high amounts of path redundancy, an observation congruent with work from Albanese & Haukos (2016) and McIntyre et al. (2018).

However, these initial observations are likely overly optimistic and may mask the influence of several ecological processes influencing species dispersal and playa network connectivity. Furthermore, as indicted by our sensitivity analysis, our modelled LCPs locations were susceptible to changes in the magnitudes of resistance value alterations. Indeed, there were no instances where overlap of LCPs among the -5, base, and +5 cases reached 50%. Thus, we feel caution is warranted when considering the transitory nature of playa wetland connectivity networks (Collins et al., 2014; McIntyre et al., 2018; Starr et al., 2016; Ruiz et al., 2014) from both a structural and functional perspective.

Structurally, coalescence was only achieved at 92.71 km, a distance that far exceeds the dispersal maxima for each of the 13 regional amphibian species considered. Furthermore, the playa clusters layer used for this study lacks information on

dynamic and local ecological conditions (e.g. hydroperiod) that are crucial for resident and migratory wildlife. Because our study assumed that all playa wetland clusters were always suitable habitat (a condition likely extremely rare; Collins et al., 2014; McIntyre et al., 2018; Ruiz et al., 2014), our results ought to be interpreted as a best-case scenario for dispersal across the region from a structural perspective.

Our results of modelled amphibian movements among the playa wetland clusters of the south- central Great Plains thus indicate that functional connectivity of amphibians within this agriculturally dominated landscape may be achievable only by spanning scales from daily movements to inter- generational dispersal. Although connections were achievable among sub-sections of the playa wetland cluster network, the individual pathways were highly dynamic in face of changing agricultural conditions (i.e., SBM vs. CCM vs. NLM). Thus, for most amphibian species the playa network is functionally a fragmented system with numerous isolated habitats.

Our results of structural and functional connectivity both indicate that the playa network is likely fragmented with respect to amphibian dispersal; however, there are several sizable sub-networks which may become important components in supporting conservation measures for amphibians. However, land-use/land-cover changes may pose challenges to the integration of conservation practices by landowners and managers for amphibians or other wildlife (Drake et al., 2017a, 2017b; McIntyre et al., 2016). Even so, landscape planning may provide an avenue by which to support structural and functional connectivity of amphibians as land-use/land-cover changes may be used to influence playa hydrology (Collins et al. 2014; Heintzman &

McIntyre, 2019; McIntyre et al., 2018; Ruiz et al., 2014), which by extension may either enhance or undermine amphibian dispersal potentials for conservation purposes (Drake et al., 2017a).

Conclusions

Our study is a first modelling foray into structural and functional connectivity of Great Plains amphibians. Our results are best understood as working hypotheses against which actual in situ studies may be compared. Until such conditions are feasible (given the logistical limitations of assessing amphibians across the Great Plains, as well as the dynamic nature of playa inundation), modelling structural and functional connectivity using a suite of approaches (Euclidean, LCP, and LRM) provides an effective means by which to examine possible outcomes of land-use/land-cover dynamics.

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Table 4.1. Description of the 13 amphibian species within the south-central Great Plains (Ramesh et al., 2012) and estimated maximum dispersal distances. Entries with # indicate adult only data, * indicate assumed adult data, " indicates mixed adult and non-adult data, ^ indicates non-adult data, and ~ indicates unknown age class status.

Species Name	Common Name	Estimated Maximum Dispersal Distance	Source(s)
Anaxyrus speciosus	Texas Toad	1 km > x > 5 km	NatureServe [bufonid toads]*
Anaxyrus cognatus (Bufo cognatus)	Great Plains Toad	≥5 km	Gray et al., 2004a"; Gray et al., 2004b"; Griffis-Kyle et al., 2011*
Anaxyrus woodhousii	Woodhouse's Toad	1 km > x > 5 km	NatureServe [bufonid toads]*
Anaxyrus debilis	Green Toad	3 km > x > 5 km	Griffis-Kyle et al., 2011*
Pseudacris clarkii	Spotted Chorus Frog	<1 km	Smith & Green, 2015# (based on *Pseudacris triseriata*, 213 m)
Gastrophryne olivacea	Great Plains Narrow-mouthed Toad	<1 km	Smith & Green, 2015~
Spea bombifrons	Plains Spadefoot	≥3 km	Gray et al., 2004a"; Gray et al., 2004b"
Spea multiplicata	New Mexico Spadefoot	≥3 km	Gray et al., 2004a"; Gray et al., 2004b"
Scaphiopus couchii	Couch's Spadefoot	<1 km	Mayhew, 1965 (400 m)^
Lithobates catesbeianus (Rana catesbeiana)	American Bullfrog	1.6 km > x > ~7-8 km	AmphibiaWeb, 2014; Lannoo, 2005*; Alex Smith & Green, 2005#~
Lithobates blairi	Plains Leopard Frog	Several km (3-8 km)	Gillis, 1975*; NatureServe [ranid frogs]*
Acris crepitans	Northern Cricket Frog	adults: 300 - 505 m -1.3 km juveniles: 100 m	AmphibiaWeb, 2014; Lannoo, 2005*; Kenney & Stearns, 2015"
Ambystoma tigrinum mavortium	Barred Tiger Salamander	≥3 km	Gray et al., 2004a"; Gray et al., 2004b"

Table 4.2. Estimated maximum adult dispersal categories of focal amphibian species.

1 km Threshold Category	**3 km Threshold Category**	**5 km Threshold Category**	**7 km Threshold Category**
Pseudacris clarkii	*Spea bombifrons*	*Anaxyrus speciosus*	*Lithobates catesbeinanus*
Gastrophryne olivacea	*Spea multiplicata*	*Anaxyrus cognatus*	
Scaphiopus couchii	*Ambystoma tigrinum mavortium*	*Anaxyrus woodhousii*	
	Acris crepitans	*Anaxyrus debilis*	
		Lithobates blairi	

Table 4.3. Cropland Data Layer and Moderate Resolution Imaging Spectroradiometer (MODIS) Irrigated Agriculture Dataset for the United States (MIrAD-US) reclassification methodology used for all models and focal years.

CDL Class Description	**SBM Class ID** *for Reclassified CDL Categories (14)*	**CCM Class ID** *for Reclassified CDL Categories (8)*	**NLM Class ID** *for Reclassified CDL Categories (13)*
Background	NoData	NoData	NoData
Corn + Sweet Corn + Orn Corn	1	1	1
Cotton	2	1	2
Sorghum	3	1	3
Durum Wheat + Spring Wheat + Winter Wheat	4	1	4
Soybeans	5	1	5
Double Crops with one or more of above categories	6	1	6
All other crops (incl. Fallow/Idle Cropland, Aquaculture, & Double Crops absent above)	7	1	7
Forest + Deciduous Forest + Evergreen Forest + Mixed Forest	8	8	8
Wetlands + Woody Wetlands + Herbaceous Wetlands	9	9	9
Open Water	10	10	10
Perennial Ice/Snow	NoData	NoData	NoData
Developed Open + Low + Med + High	11	11	11
Barren	12	12	12
Shrubland	13	13	14
Grass/Pasture	14	14	14
MIrAD-US Class Descriptions (via processing)	**SBM Class ID** *for Reclassified MIrAD-US Categories (17)*	**CCM Class ID** *for Reclassified MIrAD-US Categories (17)*	**NLM Class ID** *for Reclassified MIrAD-US Categories (17)*
Index Value of Amount of Irrigation	0	0	0
Index Value of Amount of Irrigation	6	6	6
Index Value of Amount of Irrigation	13	13	13
Index Value of Amount of Irrigation	19	19	19
Index Value of Amount of Irrigation	25	25	25
Index Value of Amount of Irrigation	31	31	31
Index Value of Amount of Irrigation	38	38	38
Index Value of Amount of Irrigation	44	44	44
Index Value of Amount of Irrigation	50	50	50
Index Value of Amount of Irrigation	56	56	56
Index Value of Amount of Irrigation	63	63	63
Index Value of Amount of Irrigation	69	69	69
Index Value of Amount of Irrigation	75	75	75
Index Value of Amount of Irrigation	81	81	81
Index Value of Amount of Irrigation	88	88	88
Index Value of Amount of Irrigation	94	94	94
Index Value of Amount of Irrigation	100	100	100

Table 4.4. Soybeans Best Model resistance value parameterization for 2008.

SBM: 2008 Resistance Values						
Data Type	**Class ID**	**Class Description**	**Cell Expansion**	**Minus 5 Case**	**Base Case**	**Plus 5 Case**
Reclassified 2008 CDL LULC	1	Corn	0	14	19	24
Reclassified 2008 CDL LULC	2	Cotton	0	6	11	16
Reclassified 2008 CDL LULC	3	Sorghum	0	8	13	18
Reclassified 2008 CDL LULC	4	Wheat	0	10	15	20
Reclassified 2008 CDL LULC	5	Soybeans	0	2	7	12
Reclassified 2008 CDL LULC	6	Double Crops (Primary)	0	12	17	22
Reclassified 2008 CDL LULC	7	Other Crops	0	18	23	28
Reclassified 2008 CDL LULC	8	Forest	0	4	9	14
Reclassified 2008 CDL LULC	9	Wetland	1	1	1	6
Reclassified 2008 CDL LULC	10	Open Water	1	1	5	10
Reclassified 2008 CDL LULC	11	Developed	1	20	25	30
Reclassified 2008 CDL LULC	12	Barren	0	22	27	32
Reclassified 2008 CDL LULC	13	Shrubland	0	16	21	26
Reclassified 2008 CDL LULC	14	Grass/Pasture	0	1	3	8
Reclassified 2007 MIrAD-US	0	Index of Amount of Irrigation	0	1	1	1
Reclassified 2007 MIrAD-US	6	Index of Amount of Irrigation	0	1	1	1
Reclassified 2007 MIrAD-US	13	Index of Amount of Irrigation	0	1	1	1
Reclassified 2007 MIrAD-US	19	Index of Amount of Irrigation	0	1	1	1
Reclassified 2007 MIrAD-US	25	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	31	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	38	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	44	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	50	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	56	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	63	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	69	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	75	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	81	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	88	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	94	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	100	Index of Amount of Irrigation	0	0	0	0

Table 4.5. Soybeans Best Model resistance value parameterization for 2016.

SBM: 2016 Resistance Values						
Data Type	**Class ID**	**Class Description**	**Cell Expansion**	**Minus 5 Case**	**Base Case**	**Plus 5 Case**
Reclassified 2016 CDL LULC	1	Corn	0	14	19	24
Reclassified 2016 CDL LULC	2	Cotton	0	6	11	16
Reclassified 2016 CDL LULC	3	Sorghum	0	8	13	18
Reclassified 2016 CDL LULC	4	Wheat	0	10	15	20
Reclassified 2016 CDL LULC	5	Soybeans	0	2	7	12
Reclassified 2016 CDL LULC	6	Double Crops (Primary)	0	12	17	22
Reclassified 2016 CDL LULC	7	Other Crops	0	18	23	28
Reclassified 2016 CDL LULC	8	Forest	0	4	9	14
Reclassified 2016 CDL LULC	9	Wetland	1	1	1	6
Reclassified 2016 CDL LULC	10	Open Water	1	1	5	10
Reclassified 2016 CDL LULC	11	Developed	1	20	25	30
Reclassified 2016 CDL LULC	12	Barren	0	22	27	32
Reclassified 2016 CDL LULC	13	Shrubland	0	16	21	26
Reclassified 2016 CDL LULC	14	Grass/Pasture	0	1	3	8
Reclassified 2012 MIrAD-US	0	Index of Amount of Irrigation	0	1	1	1
Reclassified 2012 MIrAD-US	6	Index of Amount of Irrigation	0	1	1	1
Reclassified 2012 MIrAD-US	13	Index of Amount of Irrigation	0	1	1	1
Reclassified 2012 MIrAD-US	19	Index of Amount of Irrigation	0	1	1	1
Reclassified 2012 MIrAD-US	25	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	31	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	38	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	44	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	50	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	56	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	63	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	69	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	75	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	81	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	88	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	94	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	100	Index of Amount of Irrigation	0	0	0	0

Table 4.6. Cropland Combined Model resistance value parameterization for 2008.

CCM: 2008 Resistance Values						
Data Type	**Class ID**	**Class Description**	**Cell Expansion**	**Minus 5 Case**	**Base Case**	**Plus 5 Case**
Reclassified 2008 CDL LULC	1	Cropland	0	10	15	20
Reclassified 2008 CDL LULC	8	Forest	0	4	9	14
Reclassified 2008 CDL LULC	9	Wetland	1	1	1	6
Reclassified 2008 CDL LULC	10	Open Water	1	1	5	10
Reclassified 2008 CDL LULC	11	Developed	1	20	25	30
Reclassified 2008 CDL LULC	12	Barren	0	22	27	32
Reclassified 2008 CDL LULC	13	Shrubland	0	16	21	26
Reclassified 2008 CDL LULC	14	Grass/Pasture	0	1	3	8
Reclassified 2007 MIrAD-US	0	Index of Amount of Irrigation	0	1	1	1
Reclassified 2007 MIrAD-US	6	Index of Amount of Irrigation	0	1	1	1
Reclassified 2007 MIrAD-US	13	Index of Amount of Irrigation	0	1	1	1
Reclassified 2007 MIrAD-US	19	Index of Amount of Irrigation	0	1	1	1
Reclassified 2007 MIrAD-US	25	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	31	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	38	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	44	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	50	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	56	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	63	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	69	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	75	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	81	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	88	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	94	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	100	Index of Amount of Irrigation	0	0	0	0

Table 4.7. Cropland Combined Model resistance value parameterization for 2016.

CCM: 2016 Resistance Values						
Data Type	**Class ID**	**Class Description**	**Cell Expansion**	**Minus 5 Case**	**Base Case**	**Plus 5 Case**
Reclassified 2016 CDL LULC	1	Cropland	0	10	15	20
Reclassified 2016 CDL LULC	8	Forest	0	4	9	14
Reclassified 2016 CDL LULC	9	Wetland	1	1	1	6
Reclassified 2016 CDL LULC	10	Open Water	1	1	5	10
Reclassified 2016 CDL LULC	11	Developed	1	20	25	30
Reclassified 2016 CDL LULC	12	Barren	0	22	27	32
Reclassified 2016 CDL LULC	13	Shrubland	0	16	21	26
Reclassified 2016 CDL LULC	14	Grass/Pasture	0	1	3	8
Reclassified 2012 MIrAD-US	0	Index of Amount of Irrigation	0	1	1	1
Reclassified 2012 MIrAD-US	6	Index of Amount of Irrigation	0	1	1	1
Reclassified 2012 MIrAD-US	13	Index of Amount of Irrigation	0	1	1	1
Reclassified 2012 MIrAD-US	19	Index of Amount of Irrigation	0	1	1	1
Reclassified 2012 MIrAD-US	25	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	31	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	38	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	44	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	50	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	56	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	63	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	69	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	75	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	81	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	88	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	94	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	100	Index of Amount of Irrigation	0	0	0	0

Table 4.8. Natural Lands Model resistance value parameterization for 2008.

NLM: 2008 Resistance Values						
Data Type	**Class ID**	**Class Description**	**Cell Expansion**	**Minus 5 Case**	**Base Case**	**Plus 5 Case**
Reclassified 2008 CDL LULC	1	Corn	0	14	19	24
Reclassified 2008 CDL LULC	2	Cotton	0	6	11	16
Reclassified 2008 CDL LULC	3	Sorghum	0	8	13	18
Reclassified 2008 CDL LULC	4	Wheat	0	10	15	20
Reclassified 2008 CDL LULC	5	Soybeans	0	2	7	12
Reclassified 2008 CDL LULC	6	Double Crops (Primary)	0	12	17	22
Reclassified 2008 CDL LULC	7	Other Crops	0	18	23	28
Reclassified 2008 CDL LULC	8	Forest	0	4	9	14
Reclassified 2008 CDL LULC	9	Wetland	1	1	1	6
Reclassified 2008 CDL LULC	10	Open Water	1	1	5	10
Reclassified 2008 CDL LULC	11	Developed	1	20	25	30
Reclassified 2008 CDL LULC	12	Barren	0	22	27	32
Reclassified 2008 CDL LULC	14	Natural Lands	0	1	3	8
Reclassified 2007 MIrAD-US	0	Index of Amount of Irrigation	0	1	1	1
Reclassified 2007 MIrAD-US	6	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	13	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	19	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	25	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	31	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	38	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	44	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	50	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	56	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	63	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	69	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	75	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	81	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	88	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	94	Index of Amount of Irrigation	0	0	0	0
Reclassified 2007 MIrAD-US	100	Index of Amount of Irrigation	0	0	0	0

Table 4.9. Natural Lands Model resistance value parameterization for 2016.

NLM: 2016 Resistance Values						
Data Type	**Class ID**	**Class Description**	**Cell Expansion**	**Minus 5 Case**	**Base Case**	**Plus 5 Case**
Reclassified 2016 CDL LULC	1	Corn	0	14	19	24
Reclassified 2016 CDL LULC	2	Cotton	0	6	11	16
Reclassified 2016 CDL LULC	3	Sorghum	0	8	13	18
Reclassified 2016 CDL LULC	4	Wheat	0	10	15	20
Reclassified 2016 CDL LULC	5	Soybeans	0	2	7	12
Reclassified 2016 CDL LULC	6	Double Crops (Primary)	0	12	17	22
Reclassified 2016 CDL LULC	7	Other Crops	0	18	23	28
Reclassified 2016 CDL LULC	8	Forest	0	4	9	14
Reclassified 2016 CDL LULC	9	Wetland	1	1	1	6
Reclassified 2016 CDL LULC	10	Open Water	1	1	5	10
Reclassified 2016 CDL LULC	11	Developed	1	20	25	30
Reclassified 2016 CDL LULC	12	Barren	0	22	27	32
Reclassified 2016 CDL LULC	14	Natural Lands	0	1	3	8
Reclassified 2012 MIrAD-US	0	Index of Amount of Irrigation	0	1	1	1
Reclassified 2012 MIrAD-US	6	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	13	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	19	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	25	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	31	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	38	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	44	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	50	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	56	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	63	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	69	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	75	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	81	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	88	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	94	Index of Amount of Irrigation	0	0	0	0
Reclassified 2012 MIrAD-US	100	Index of Amount of Irrigation	0	0	0	0

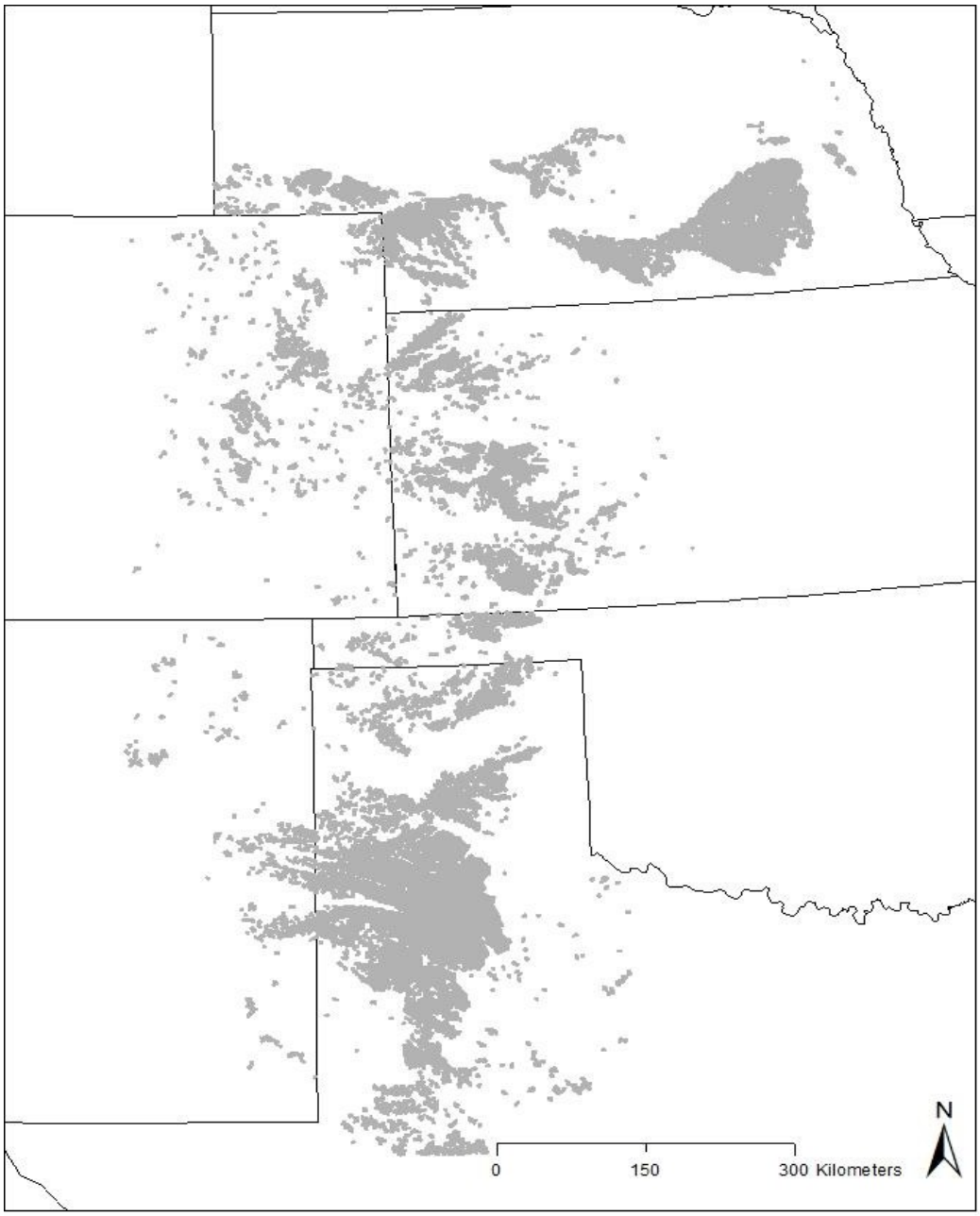

Figure 4.1. Distribution of the 904 playa wetland clusters (gray polygons) as defined by the Playa Lakes Joint Venture within the Great Plains of North America.

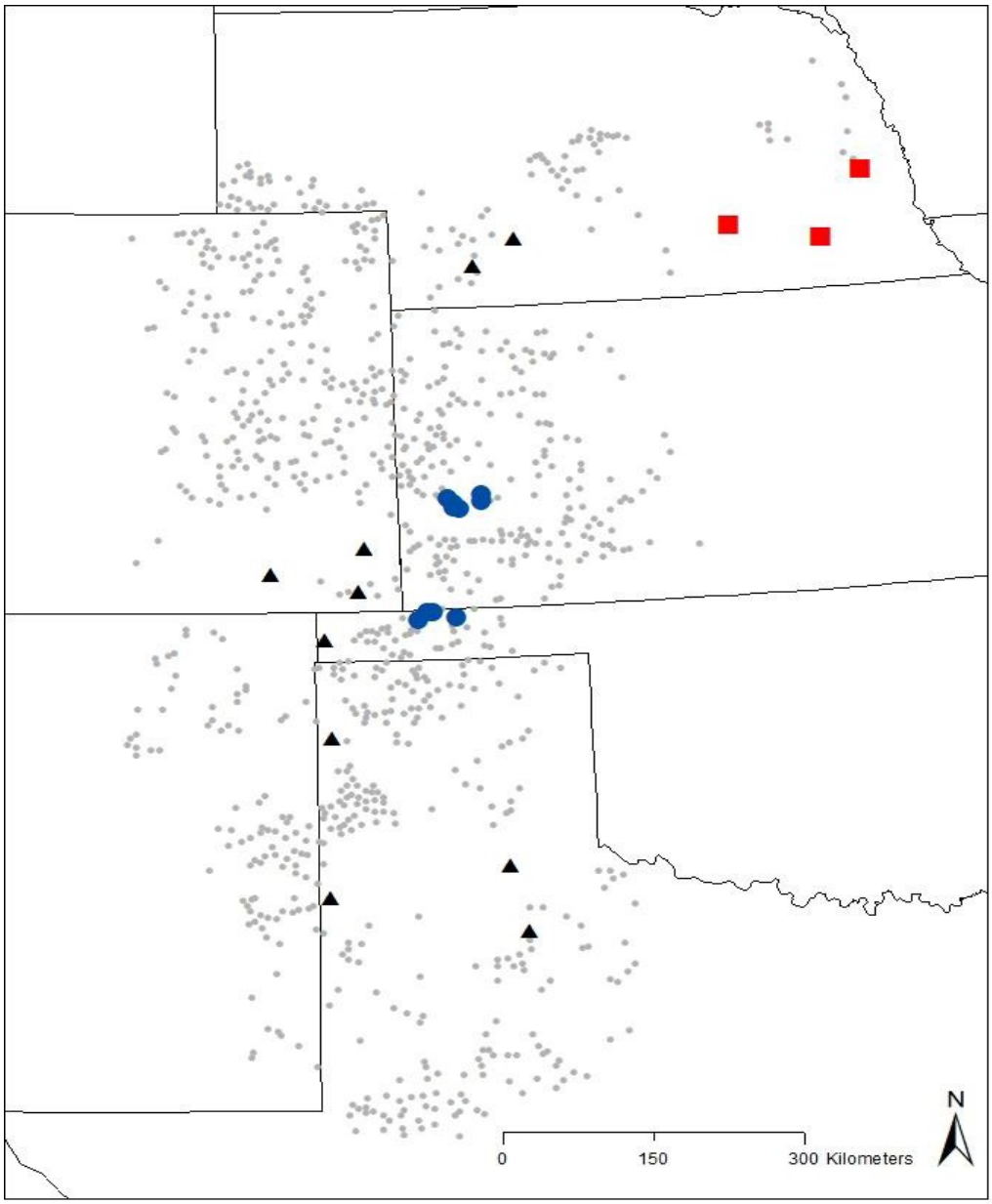

Figure 4.2. Distribution of playa wetland cluster centroids (gray dots) with locations of the 10 top-ranked stepping-stones (black triangles), hubs (blue circles), and all three cutpoints (red squares) at the coalescence distance of 92.71 km.

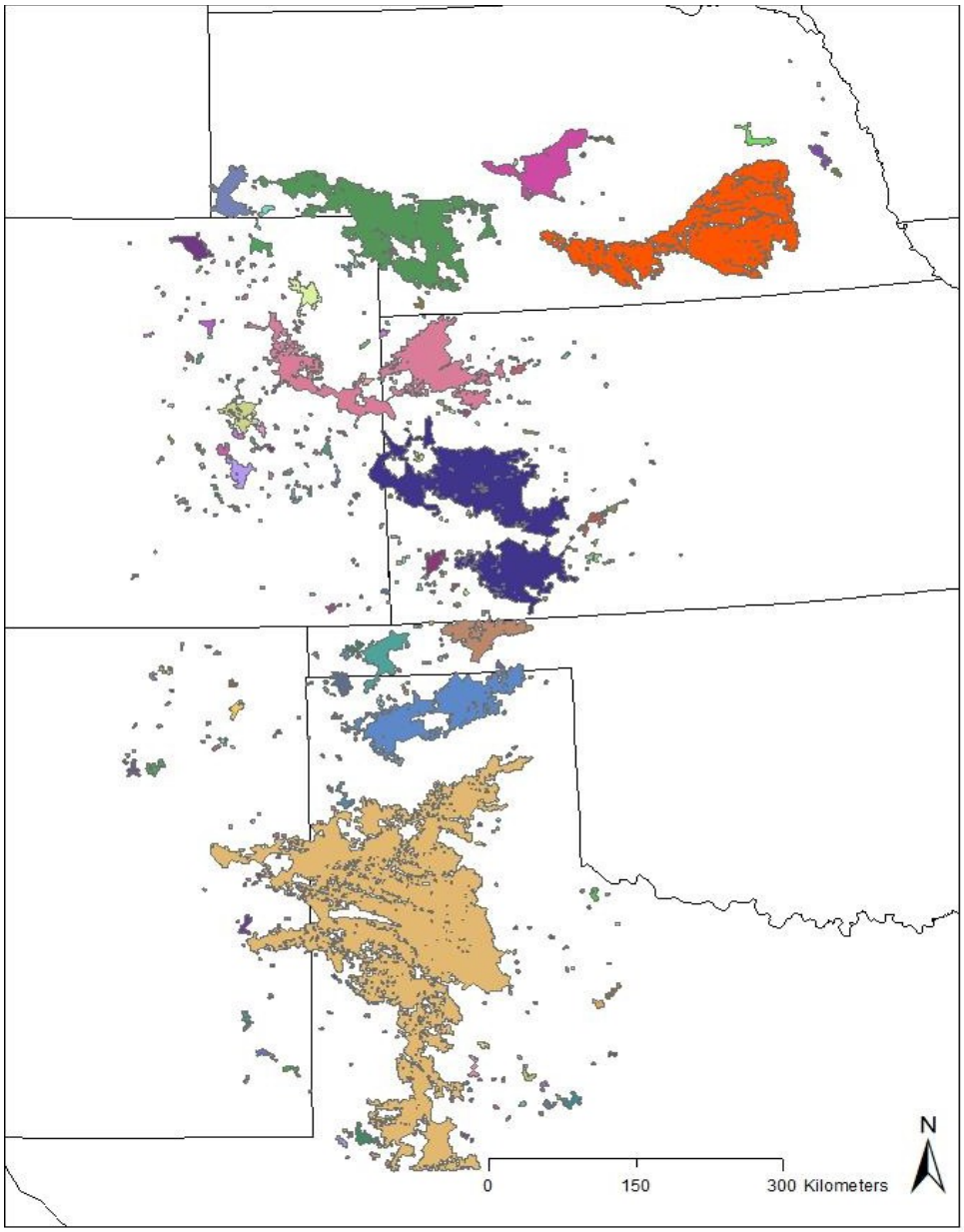

Figure 4.3. Distribution of 435 playa wetland cluster sub-networks at a 15 km dispersal threshold (roughly twice the maximum dispersal distance of the American Bullfrog). Each cluster separated by >15 km is depicted in a different color. Although some large sub-networks are visible, most playa wetland clusters exist in relative isolation.

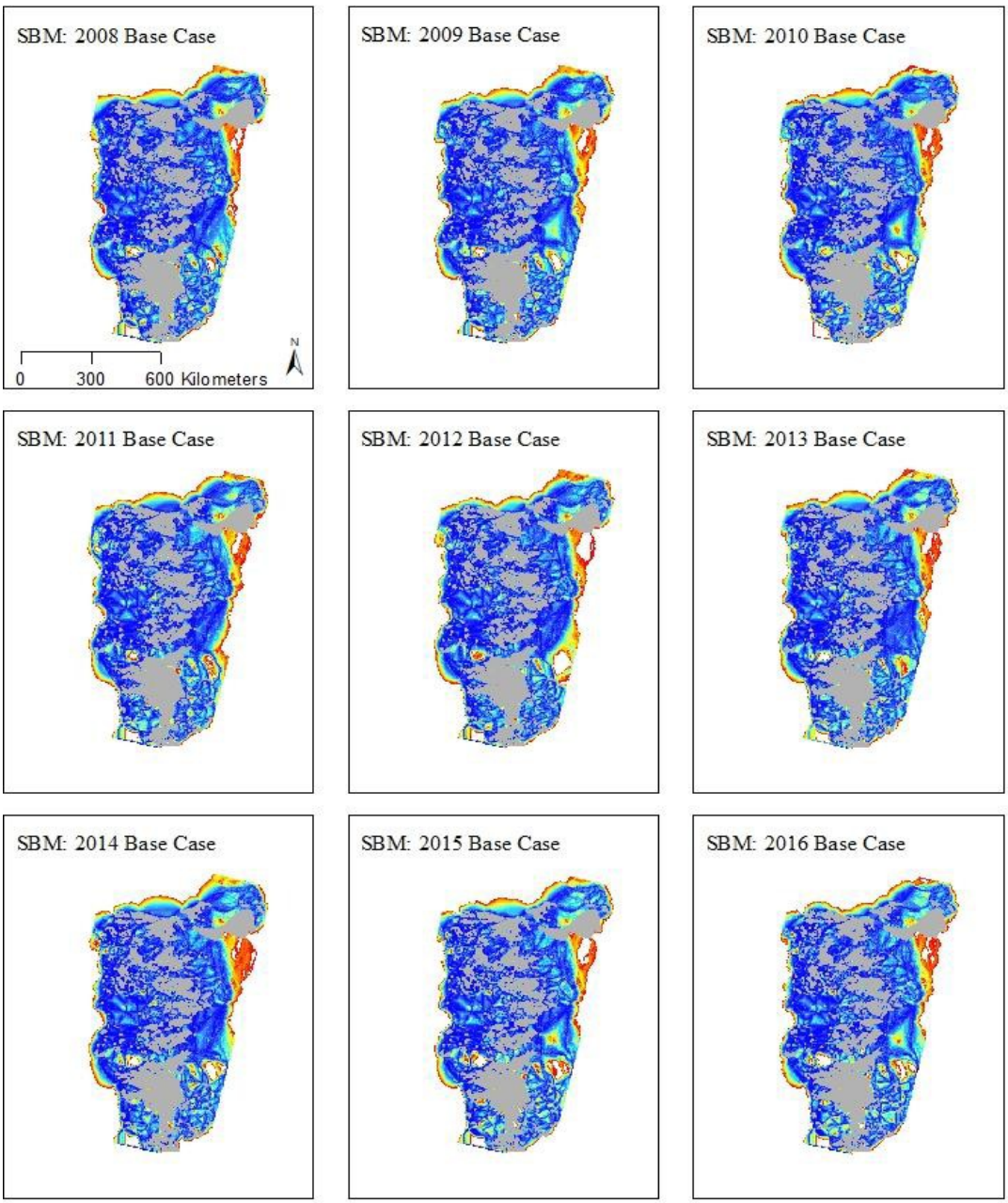

Figure 4.4. Landscape Resistance Modelling output for the Soybean Best Model base case from 2008-2016, with playa wetland clusters in gray. Areas of low resistance are in "cool" colors, and areas of high resistance are in "warm" colors.

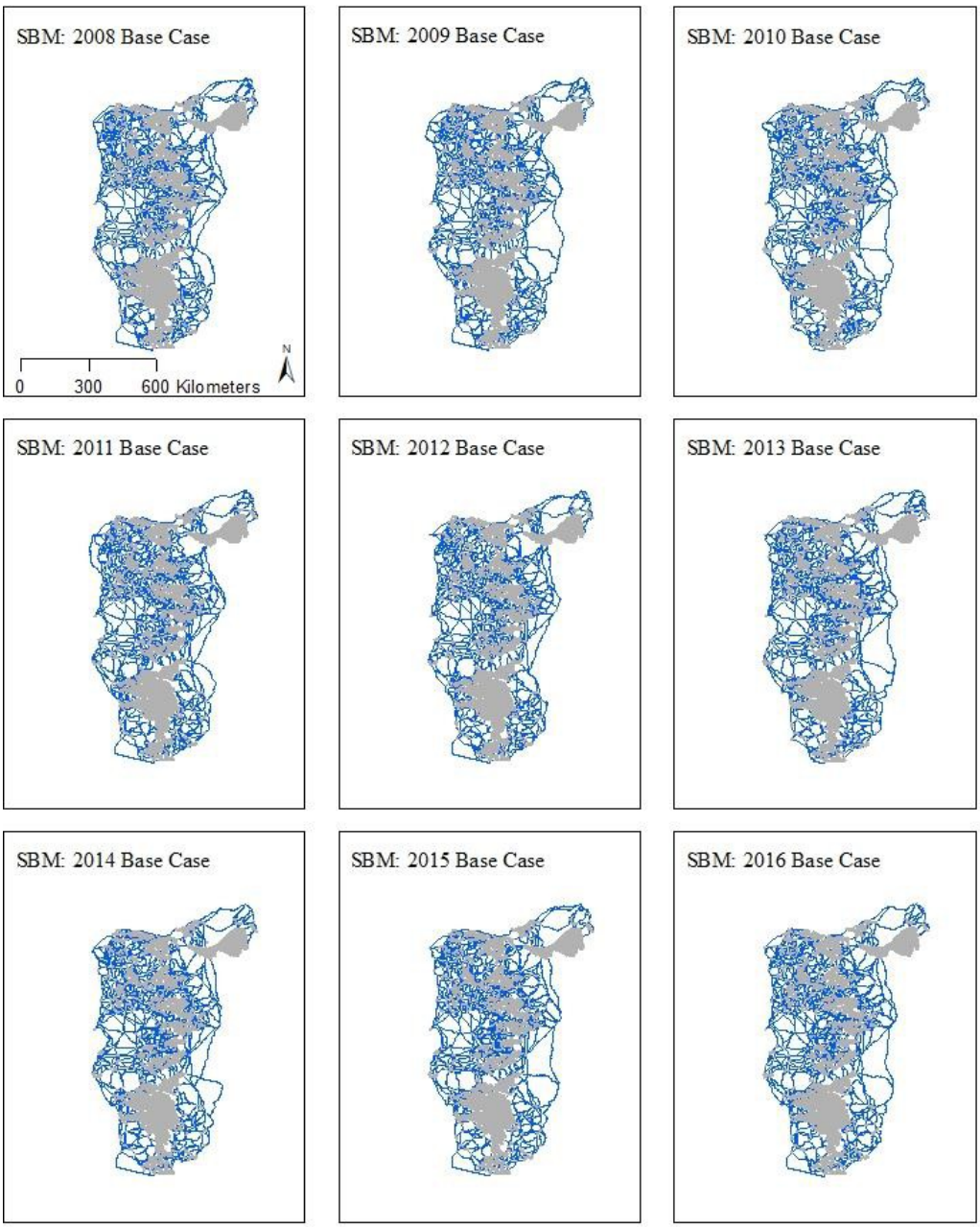

Figure 4.5. Least-Cost Path output for the Soybeans Best Model base case from 2008-2016, with playa wetland clusters in gray. Blue lines indicate locations of Least-Cost Paths among playa wetland clusters.

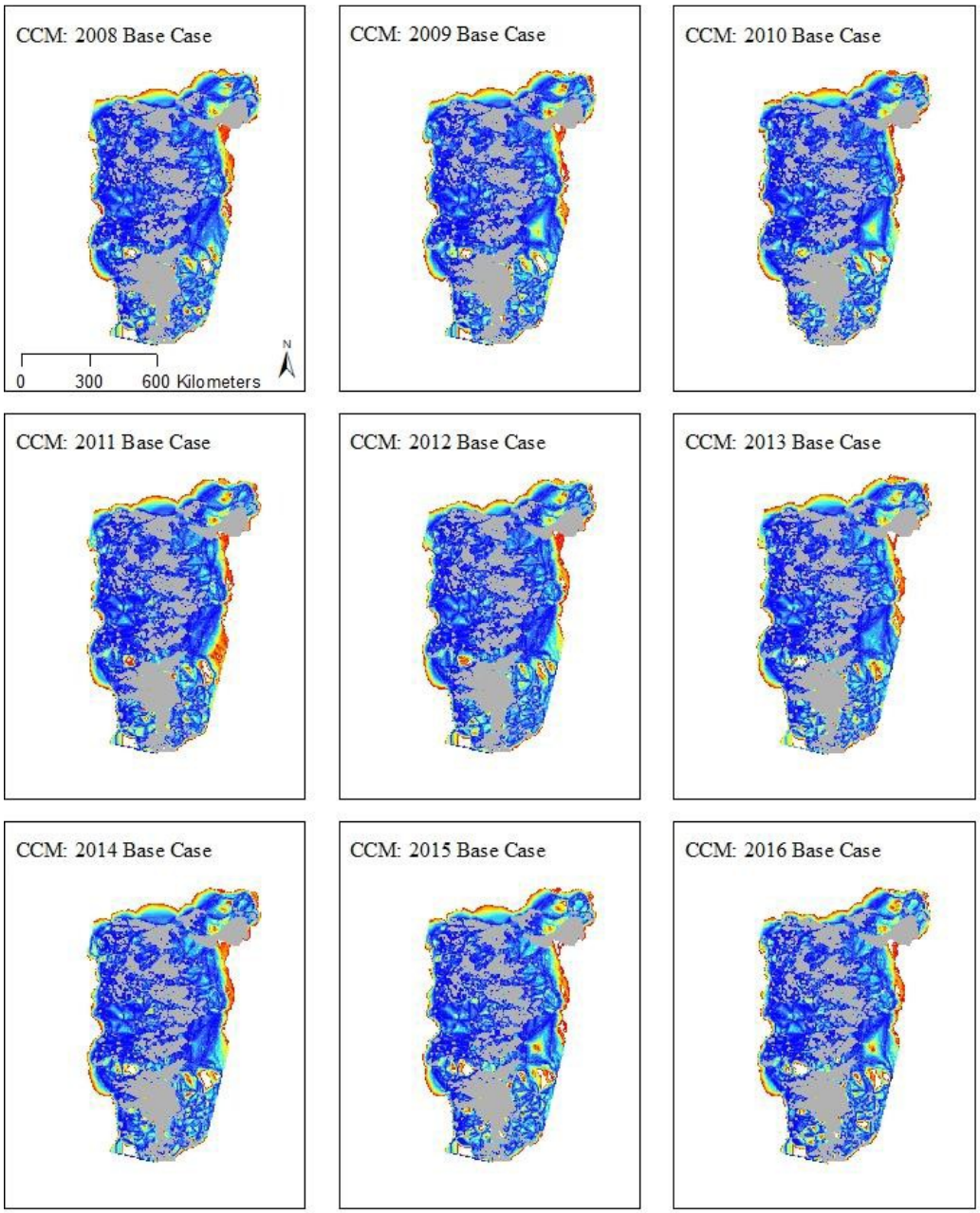

Figure 4.6. Landscape Resistance Modelling output for the Cropland Combined Model base case from 2008-2016, with playa wetland clusters in gray. Areas of low resistance are in “cool” colors, and areas of high resistance are in “warm” colors.

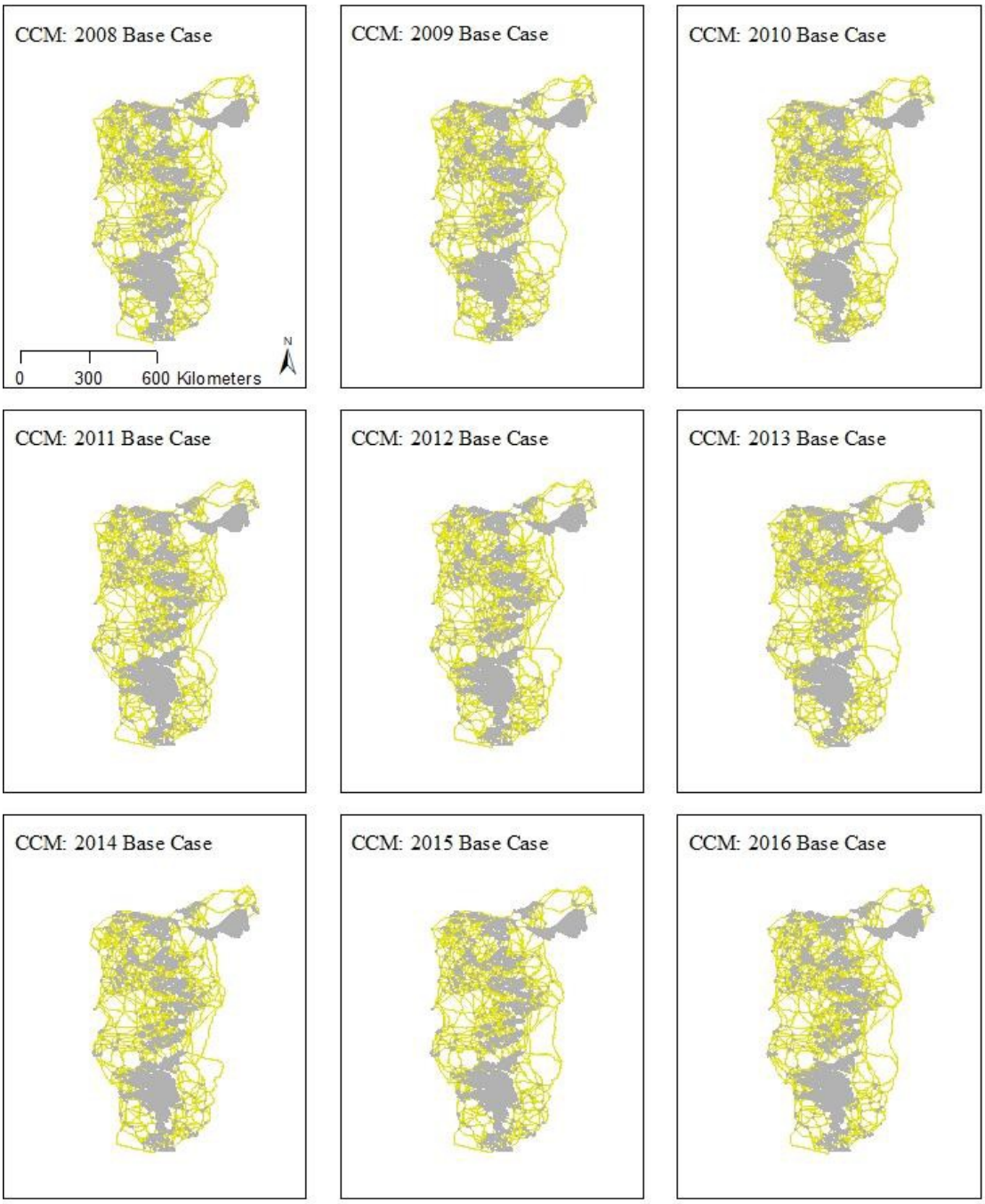

Figure 4.7. Least-Cost Path output for the Cropland Combined Model base case from 2008-2016, with playa wetland clusters in gray. Yellow lines indicate locations of Least-Cost Paths among playa wetland clusters.

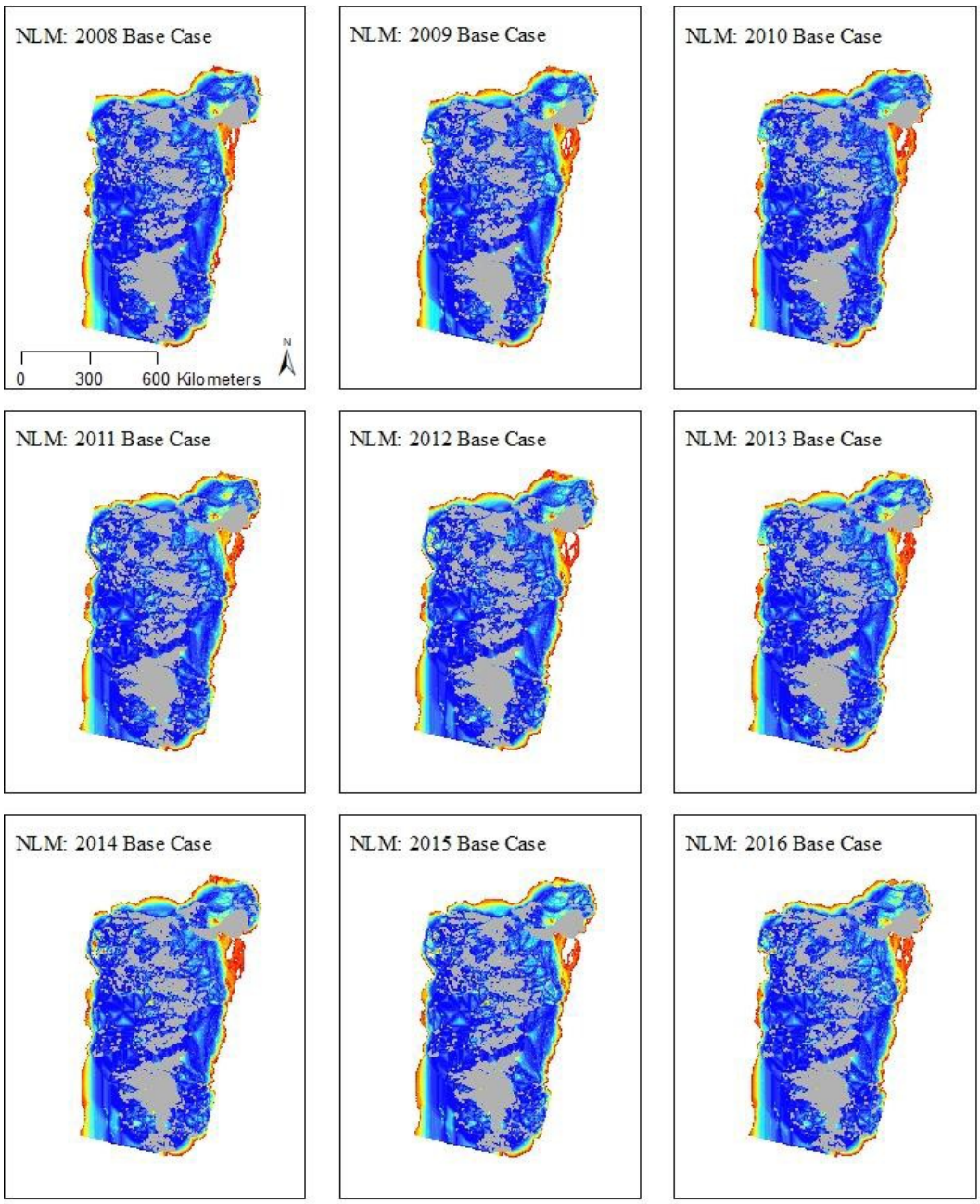

Figure 4.8. Landscape Resistance Modelling output for the Natural Lands Model base case from 2008-2016, with playa wetland clusters in gray. Areas of low resistance are in "cool" colors, and areas of high resistance are in "warm" colors.

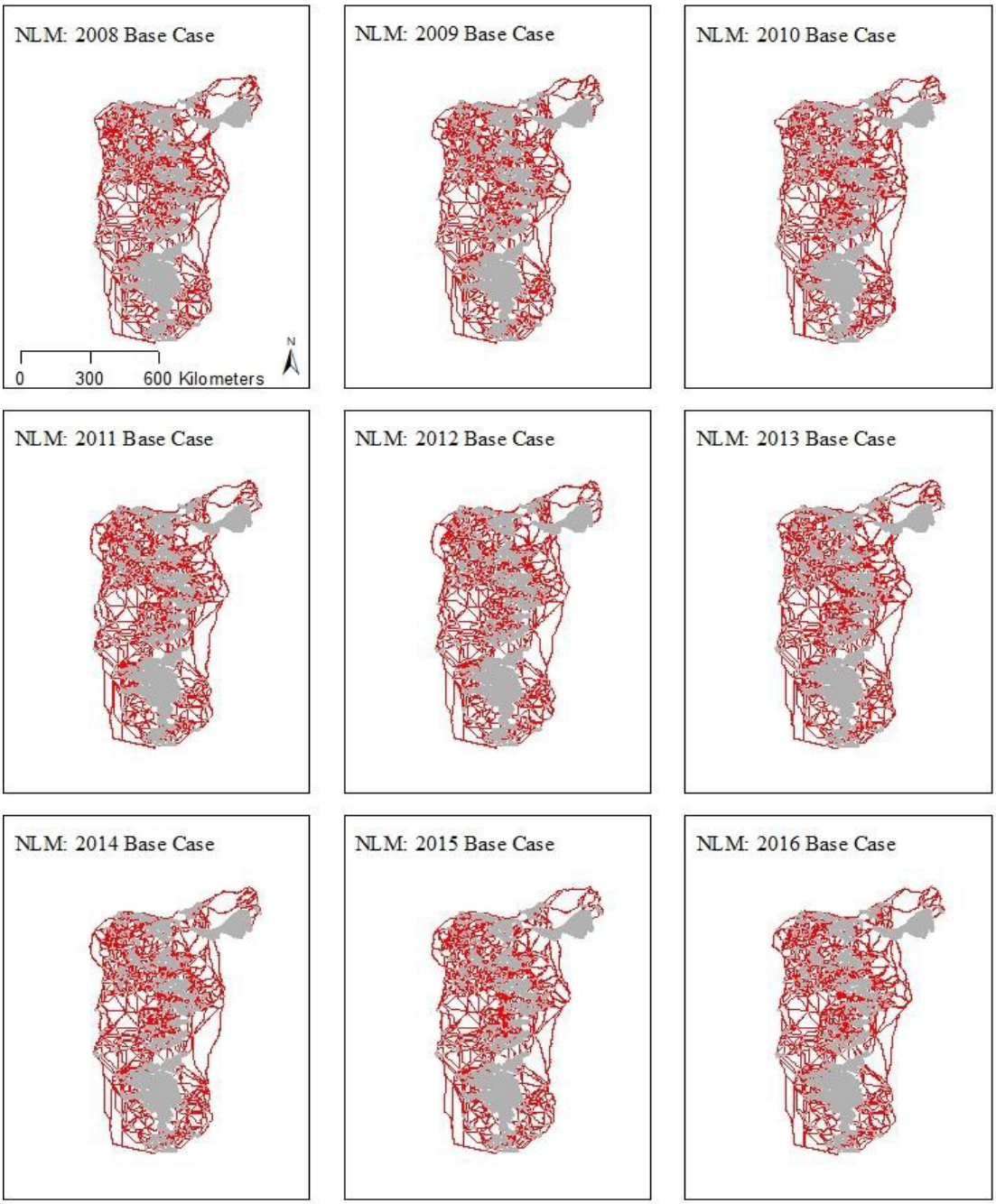

Figure 4.9. Least-Cost Path output for the Natural Lands Model base case from 2008-2016, with playa wetland clusters in gray. Red lines indicate locations of Least-Cost Paths among playa wetland clusters.

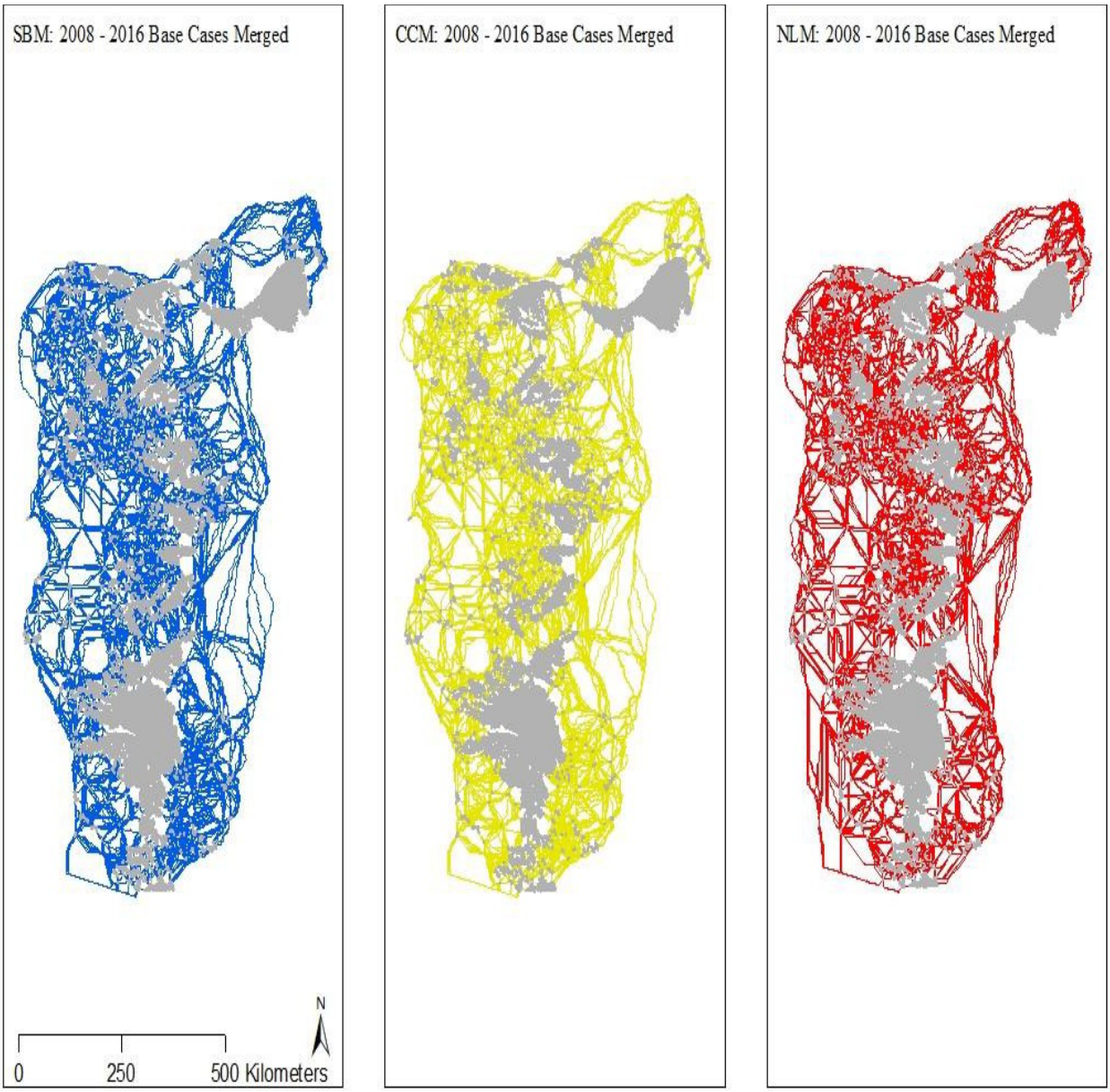

Figure 4.10. Merged Least-Cost Path locations 2008-2016 by base case, with playa wetland clusters in gray. Areas of thicker blue, yellow, and red lines indicate higher degrees of Least-Cost Path overlap among Soybeans Best Model, Cropland Combined Model, and Natural Lands Model base cases, respectively.

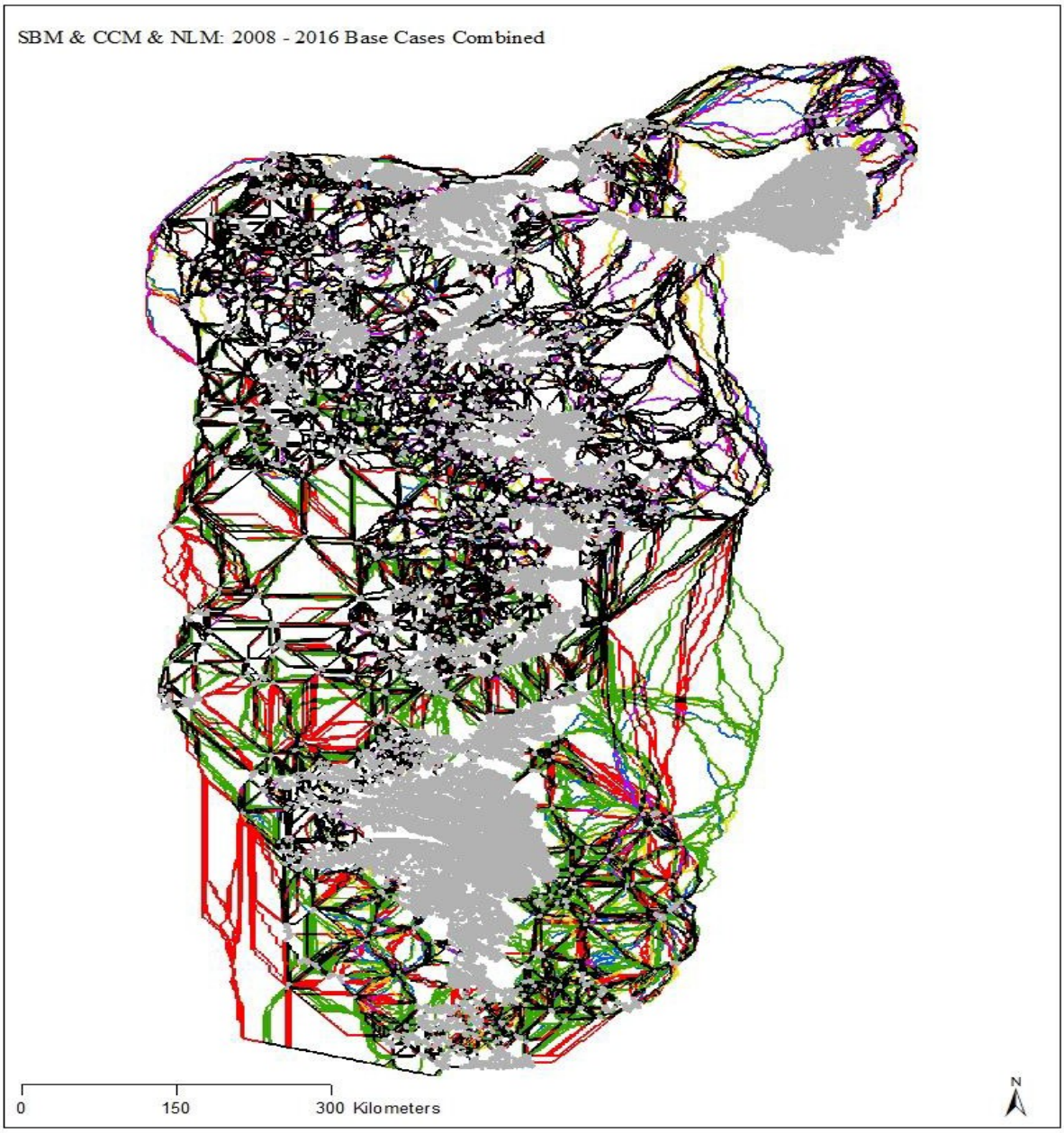

Figure 4.11. Combined LCP locations 2008-2016 among all base cases, with playa wetland clusters in gray. Least-Cost Paths overlapped by 57% among all base case models (black lines), with 24% of Least-Cost Paths overlapping with at least one other base case model (green lines: SBM and CCM Least-Cost Paths, orange lines: CCM and NLM Least-Cost Paths, purple lines: SBM and NLM Least-Cost Paths).

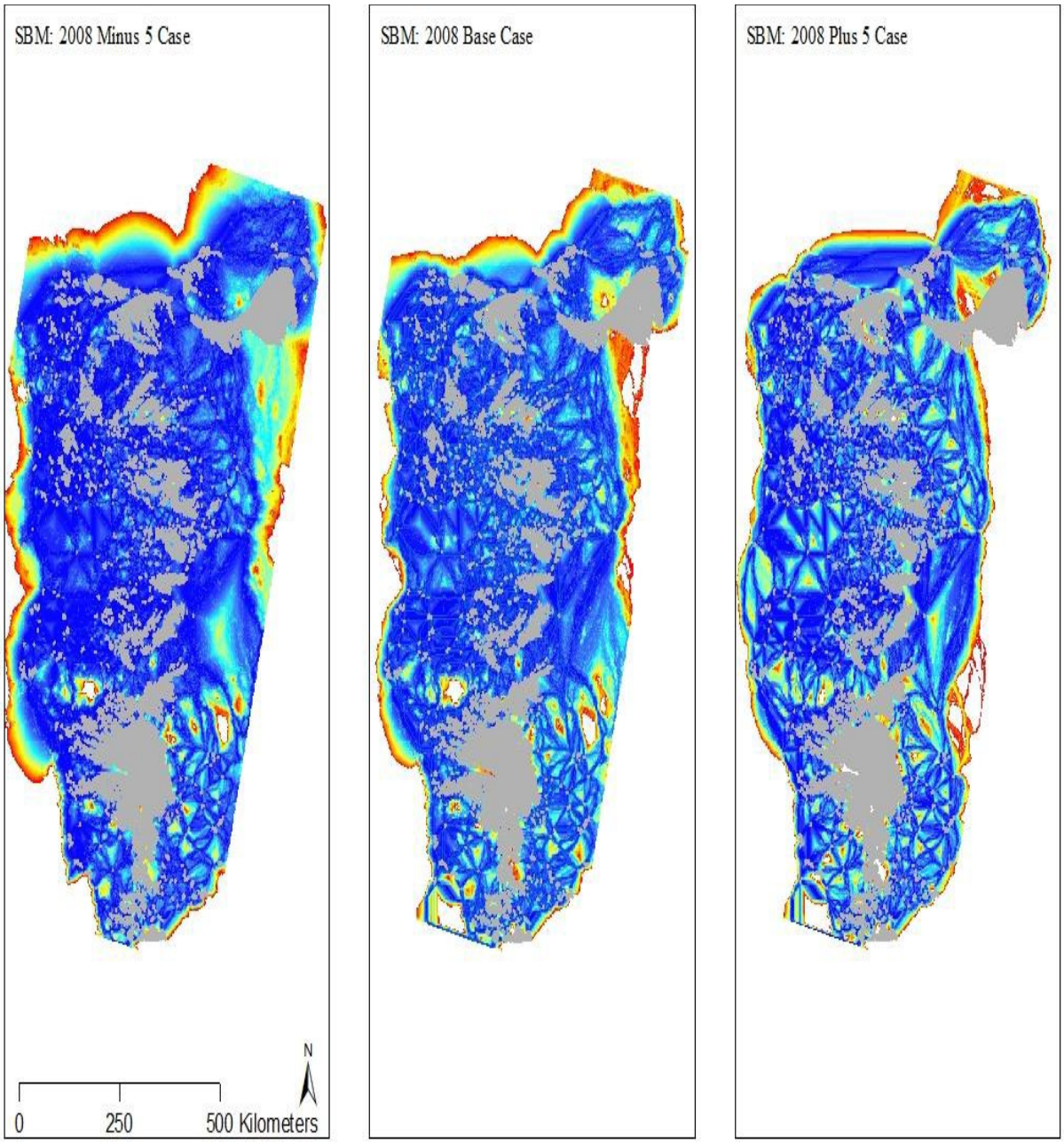

Figure 4.12. Landscape Resistance Modelling output of the Soybeans Best Model sensitivity analysis using the 2008 Minus 5 Case, the 2008 Base Case, and the 2008 Plus 5 Case. Areas of low resistance are in "cool" colors, and areas of high resistance are in "warm" colors, with playa wetland clusters in gray.

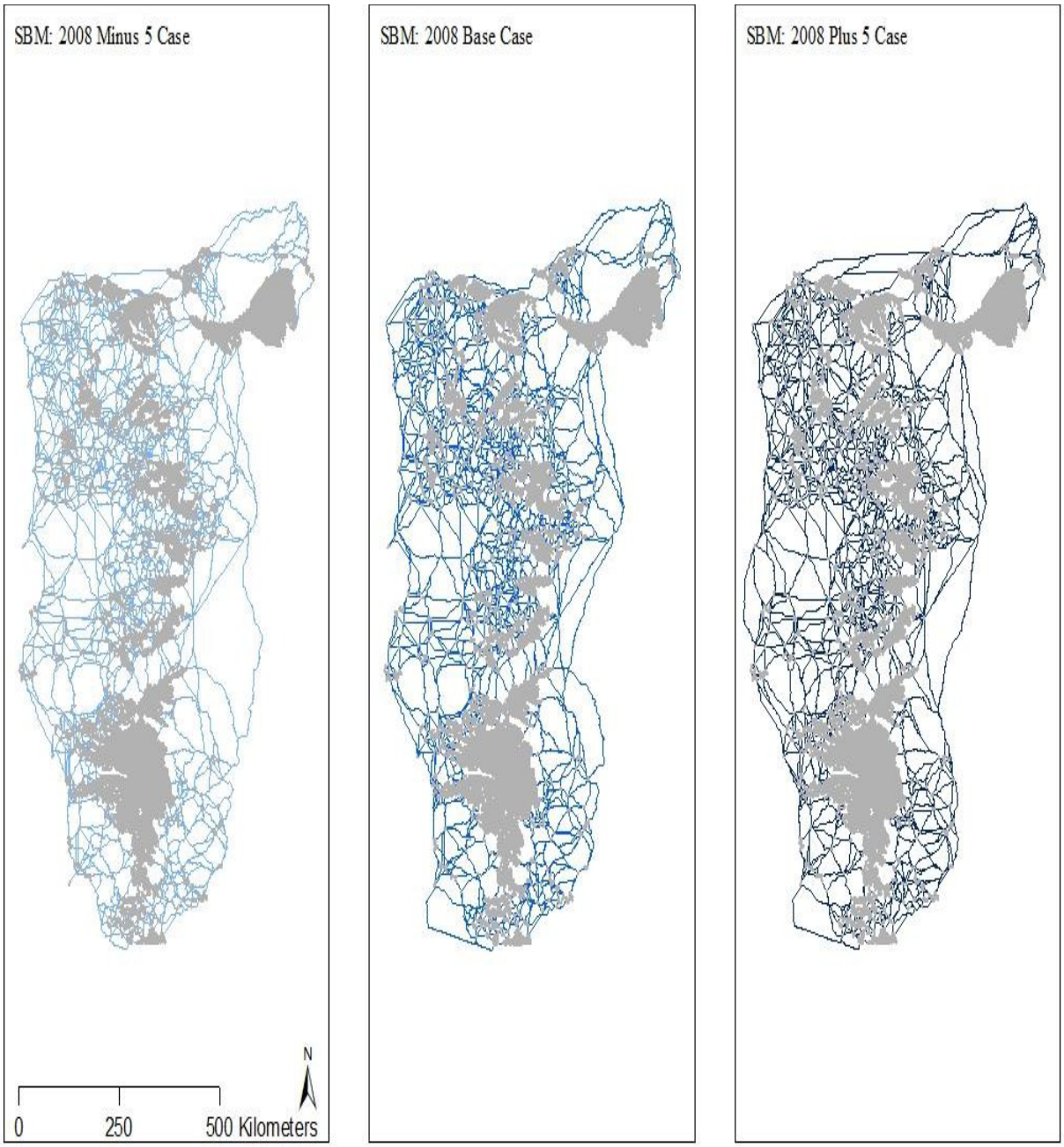

Figure 4.13. Least-Cost Path output for the Soybean Best Model sensitivity analysis using the using the 2008 Minus 5 Case, the 2008 Base Case, and the 2008 Plus 5 Case. Blue lines (shaded from light to dark, respectively) indicate locations of Least-Cost Path linkages among playa wetland clusters in gray.

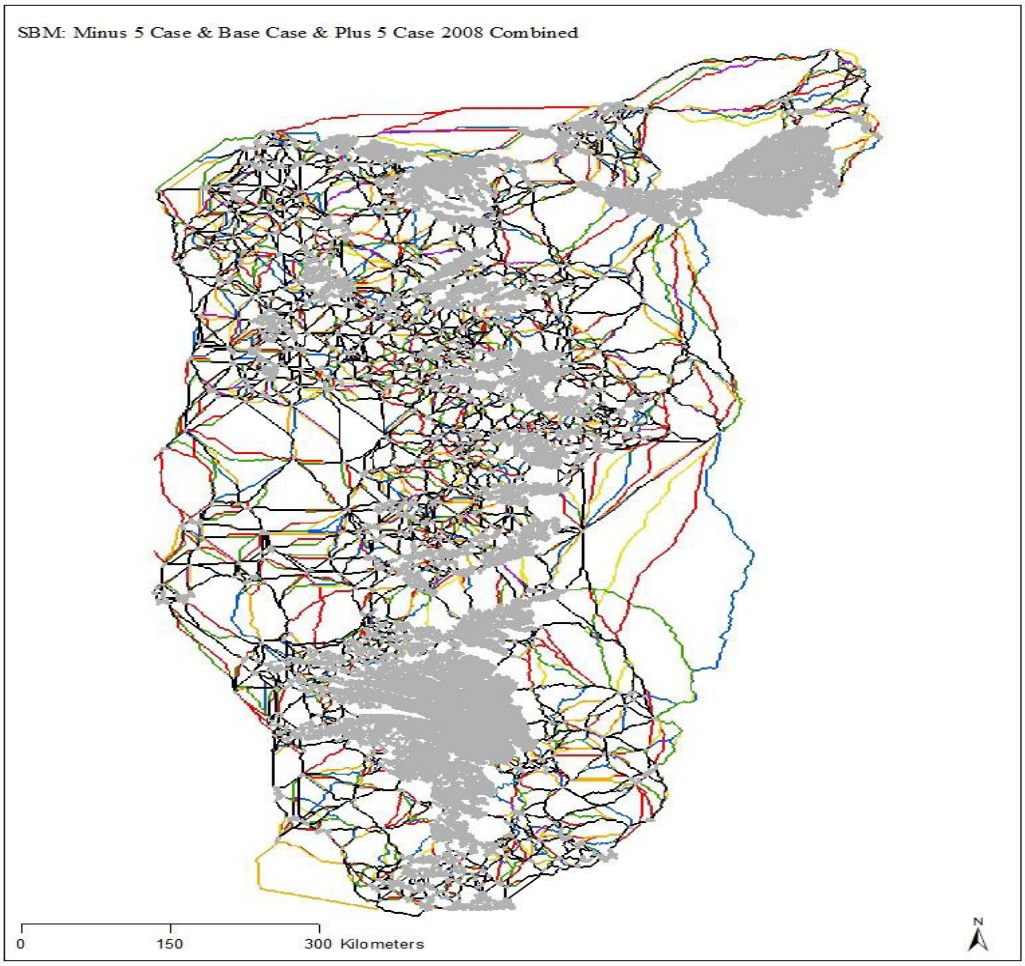

Figure 4.14. Combined LCP locations for the Soybean Best Model sensitivity analysis using the 2008 Minus 5 Case (blue lines), 2008 Base Case (yellow lines), and 2008 Plus 5 Case (red lines), with playa wetland clusters in gray. Least-Cost Paths overlapped 45% among the 2008 Minus 5 Case, 2008 Base Case, and 2008 Plus 5 Case (black lines), whereas 23% of the remaining Least-Cost Paths overlapped with at least one other model (green lines: Minus 5 Case and Base Case Least-Cost Paths, orange lines: Base Case and Plus 5 Case Least-Cost Paths, purple lines: Minus 5 Case and Plus 5 Case Least-Cost Paths).

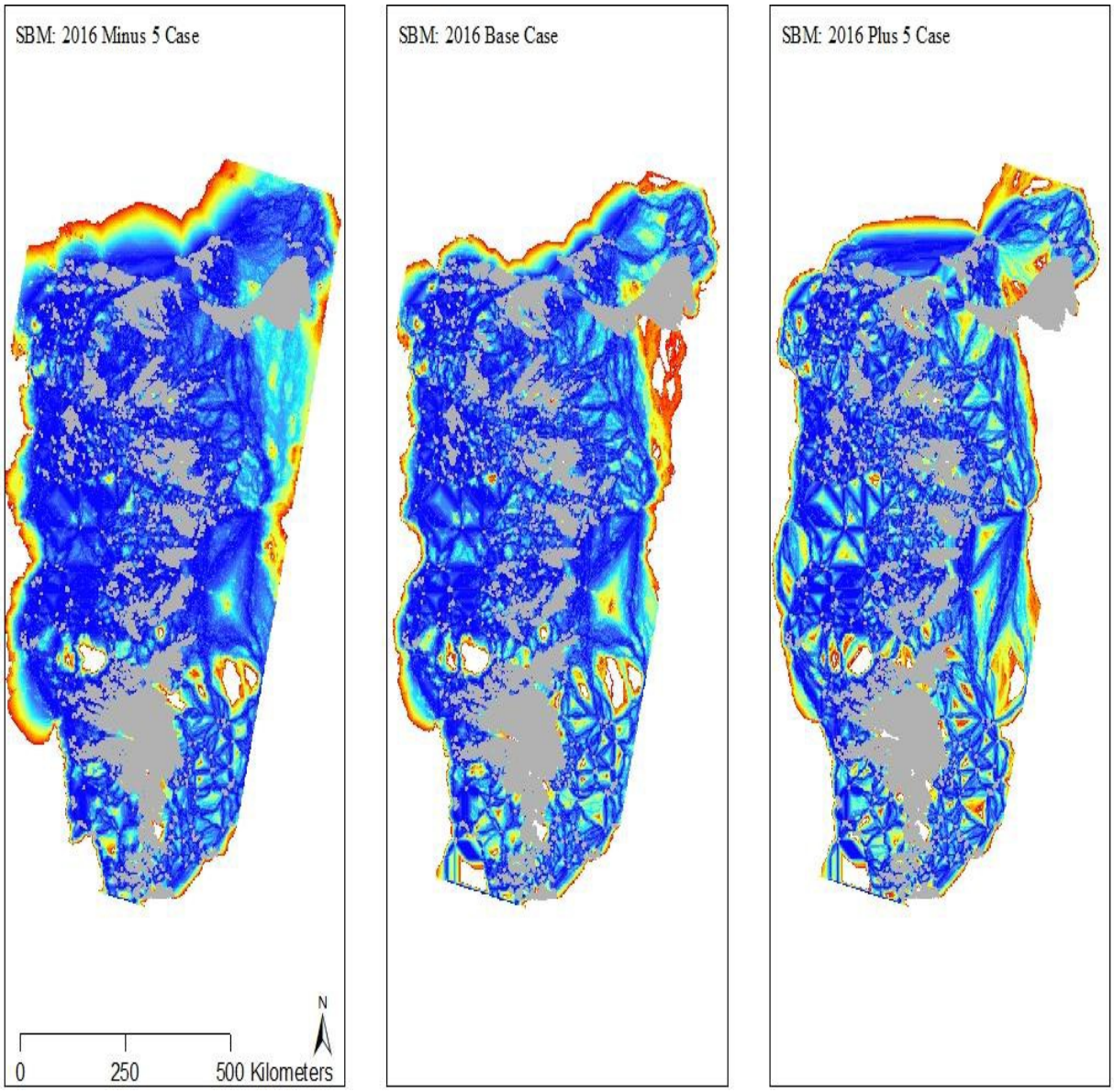

Figure 4.15. Landscape Resistance Modelling output of the Soybean Best Model sensitivity analysis using the 2016 Minus 5 Case, the 2016 Base Case, and the 2016 Plus 5 Case. Areas of low resistance are in "cool" colors, and areas of high resistance are in "warm" colors, with playa wetland clusters in gray.

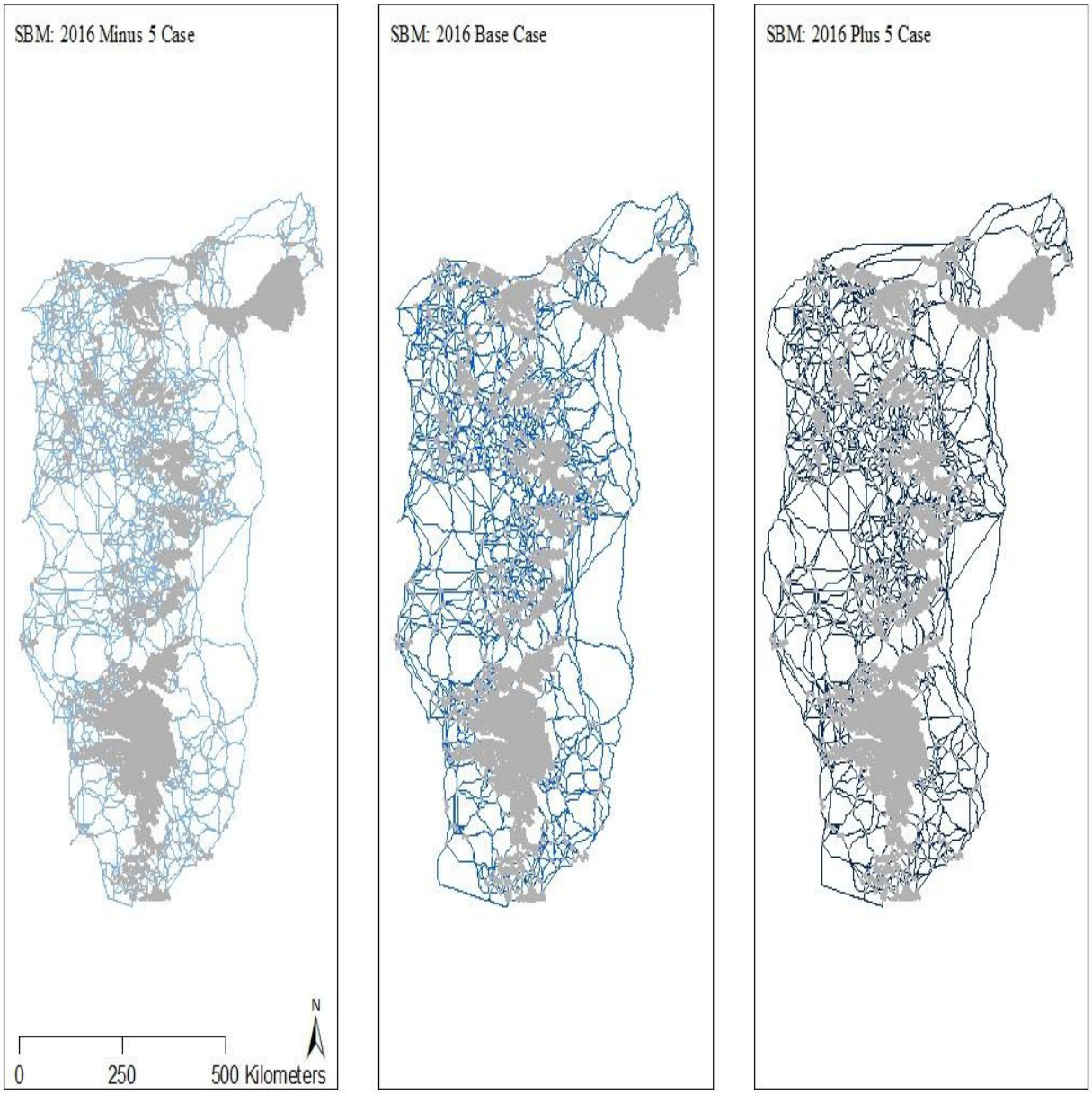

Figure 4.16. Least-Cost Path output for the Soybeans Best Model sensitivity analysis using the 2016 Minus 5 Case, the 2015 Base Case, and the 2016 Plus 5 Case. Blue lines (shaded from light to dark, respectively) indicate locations of Least-Cost Path linkages among playa wetland clusters in gray.

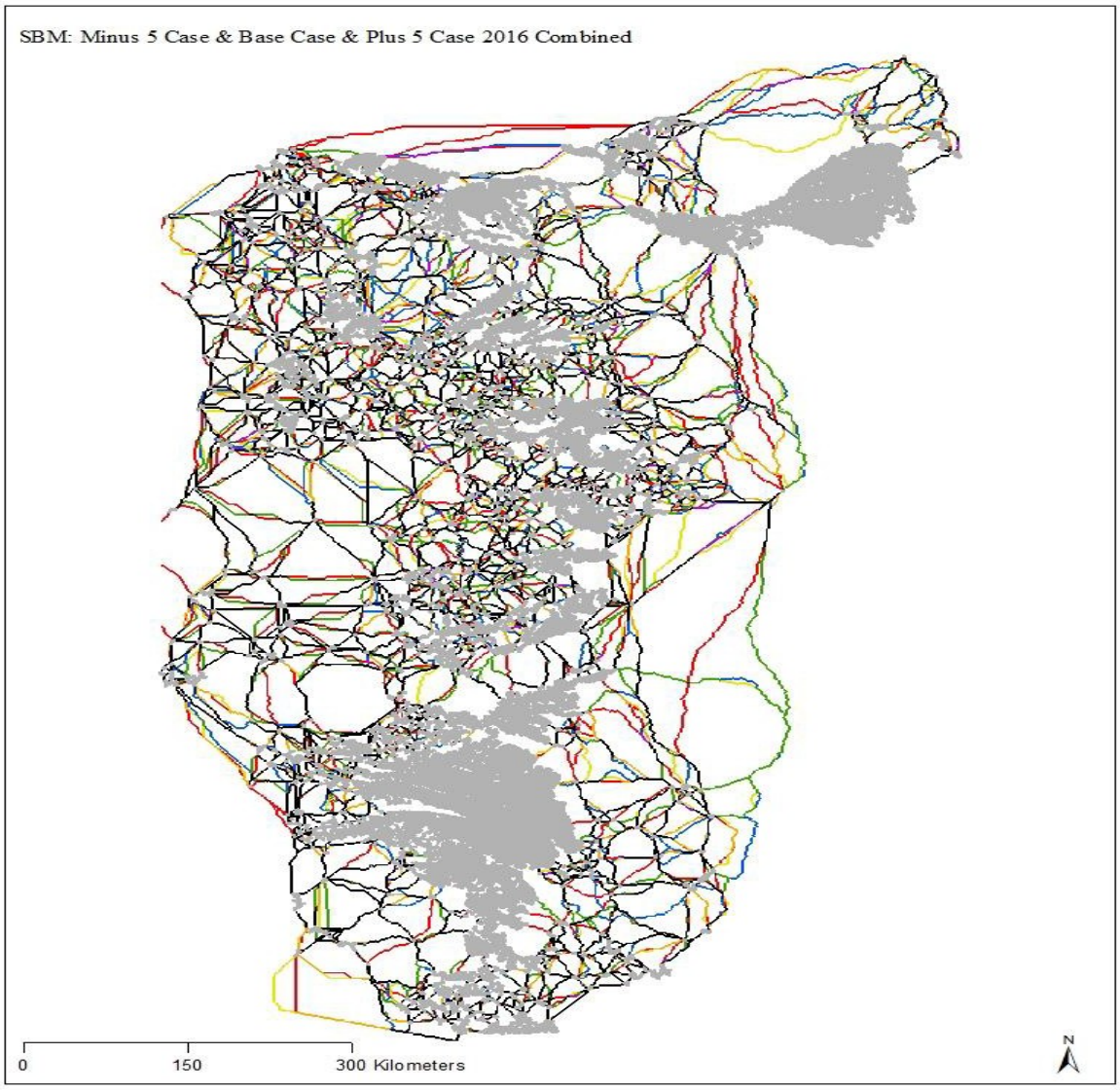

Figure 4.17. Combined Least-Cost Path locations for the Soybean Best Model sensitivity analysis using the 2016 Minus 5 Case (blue lines), 2016 Base Case (yellow lines), and 2016 Plus 5 Case (red lines), with playa wetland clusters in gray. Least-Cost Paths overlapped 46% among the 2016 Minus 5 Case, 2016 Base Case, and 2016 Plus 5 Case (black lines), whereas 23% of the remaining Least-Cost Paths overlapped with at least one other model (green lines: Minus 5 Case and Base Case Least-Cost Paths, orange lines: Base Case and Plus 5 Case Least-Cost Paths, purple lines: Minus 5 Case and Plus 5 Case Least-Cost Paths).

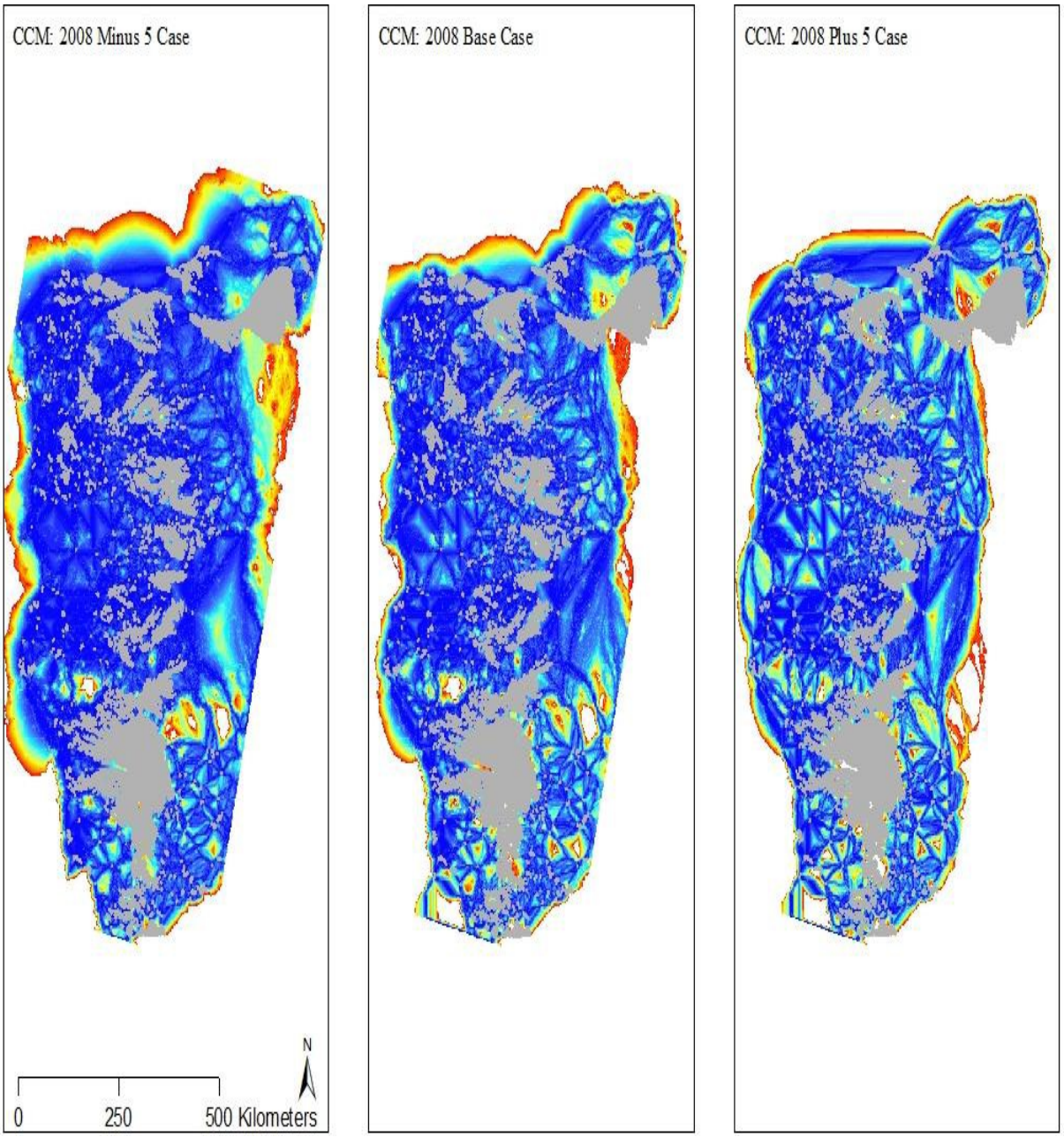

Figure 4.18. Landscape Resistance Modelling output of the Cropland Combined Model sensitivity analysis using the 2008 Minus 5 Case, the 2008 Base Case, and the 2008 Plus 5 Case. Areas of low resistance are in "cool" colors, and areas of high resistance are in "warm" colors, with playa wetland clusters in gray.

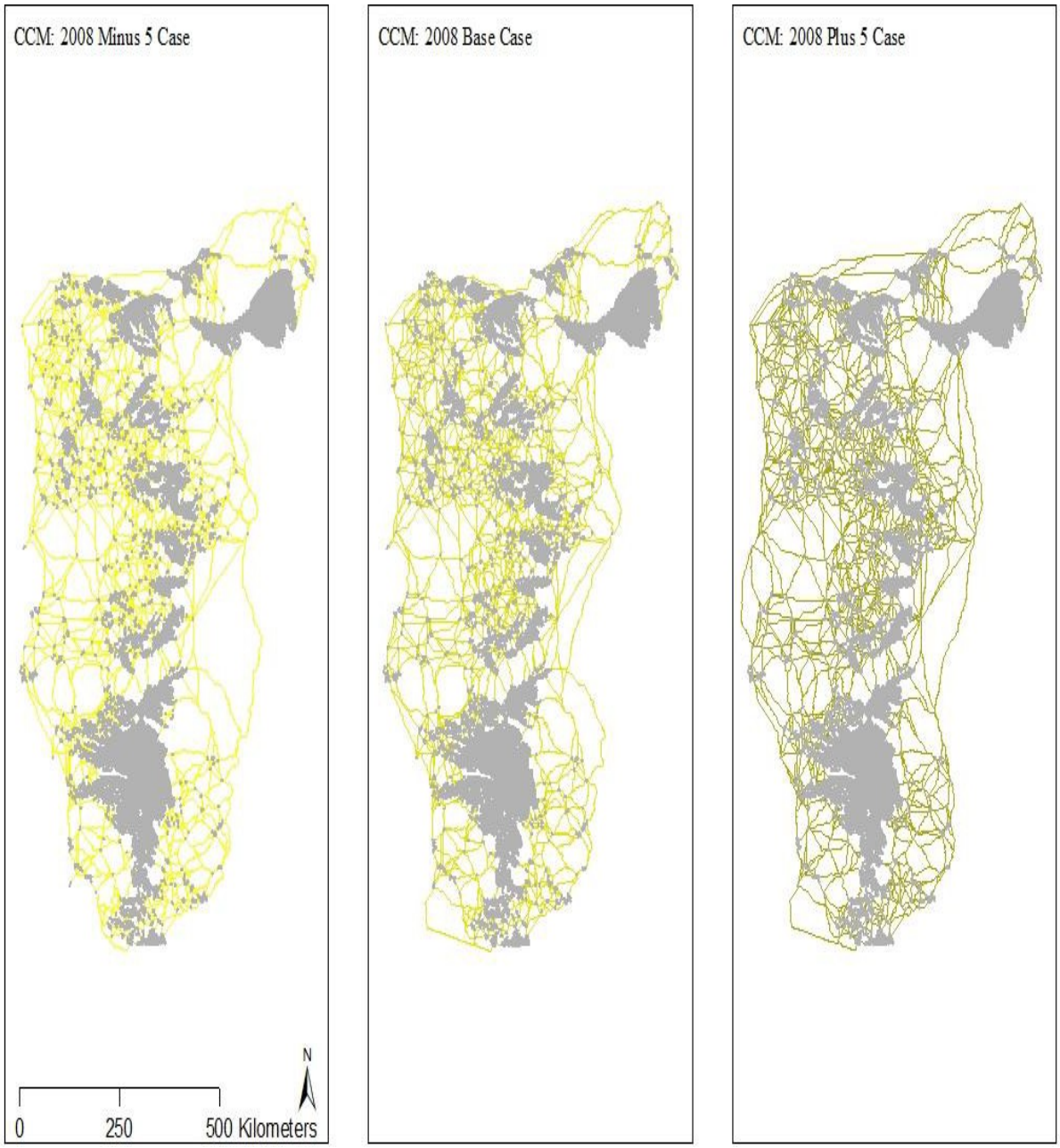

Figure 4.19. Least-Cost Path output for the Cropland Combined Model sensitivity analysis using the using the 2008 Minus 5 Case, the 2008 Base Case, and the 2008 Plus 5 Case. Yellow lines (shaded from light to dark, respectively) indicate locations of Least-Cost Path linkages among playa wetland clusters in gray.

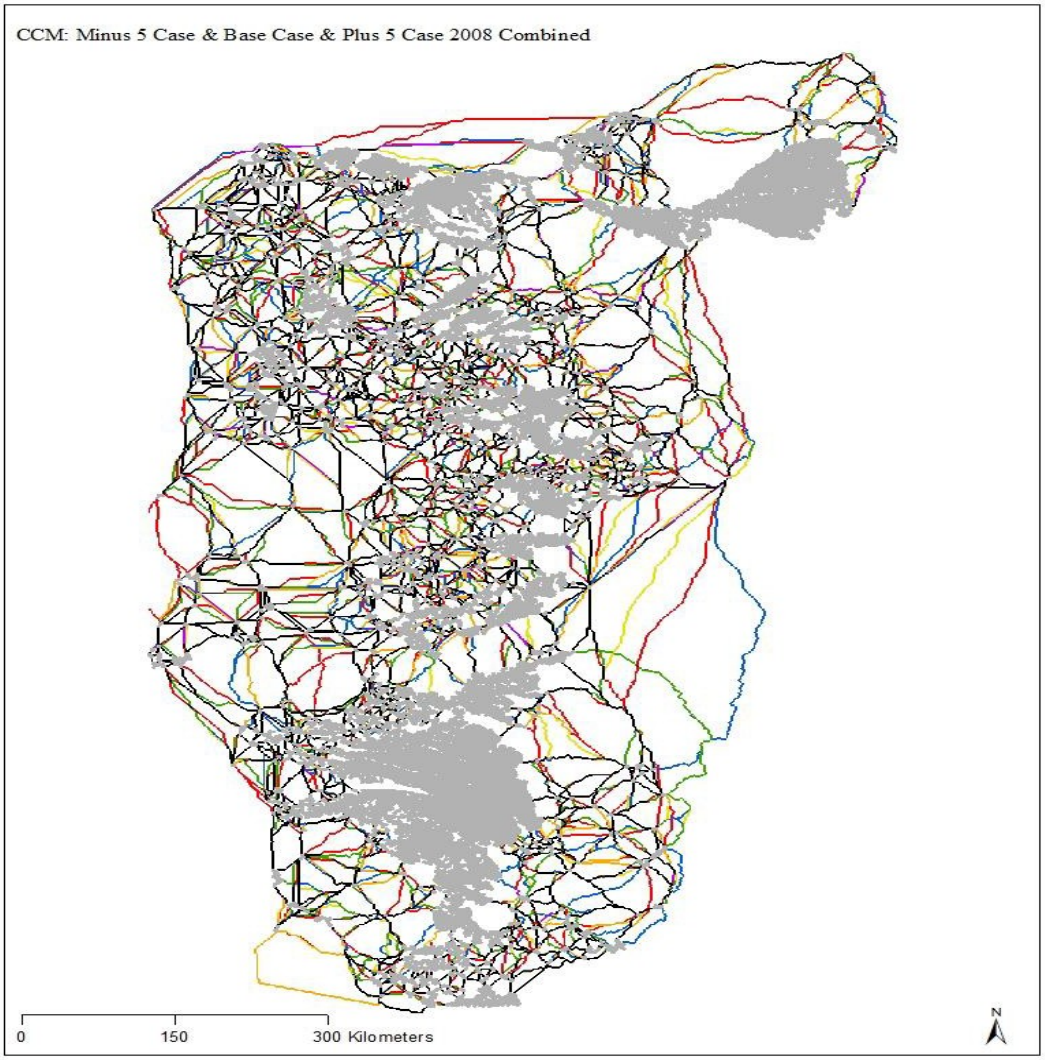

Figure 4.20. Combined Least-Cost Path locations for the Cropland Combined Model sensitivity analysis using the 2008 Minus 5 Case (blue lines), 2008 Base Case (yellow lines), and 2008 Plus 5 Case (red lines) with playa wetland clusters in gray. Least-Cost Paths overlapped 45% among the 2008 Minus 5 Case, 2008 Base Case, and 2008 Plus 5 Case (black lines), whereas 22% of remaining Least-Cost Paths overlapped with at least one other model (green lines: Minus 5 Case and Base Case Least-Cost Paths, orange lines: Base Case and Plus 5 Case Least-Cost Paths, purple lines: Minus 5 Case and Plus 5 Case Least-Cost Paths).

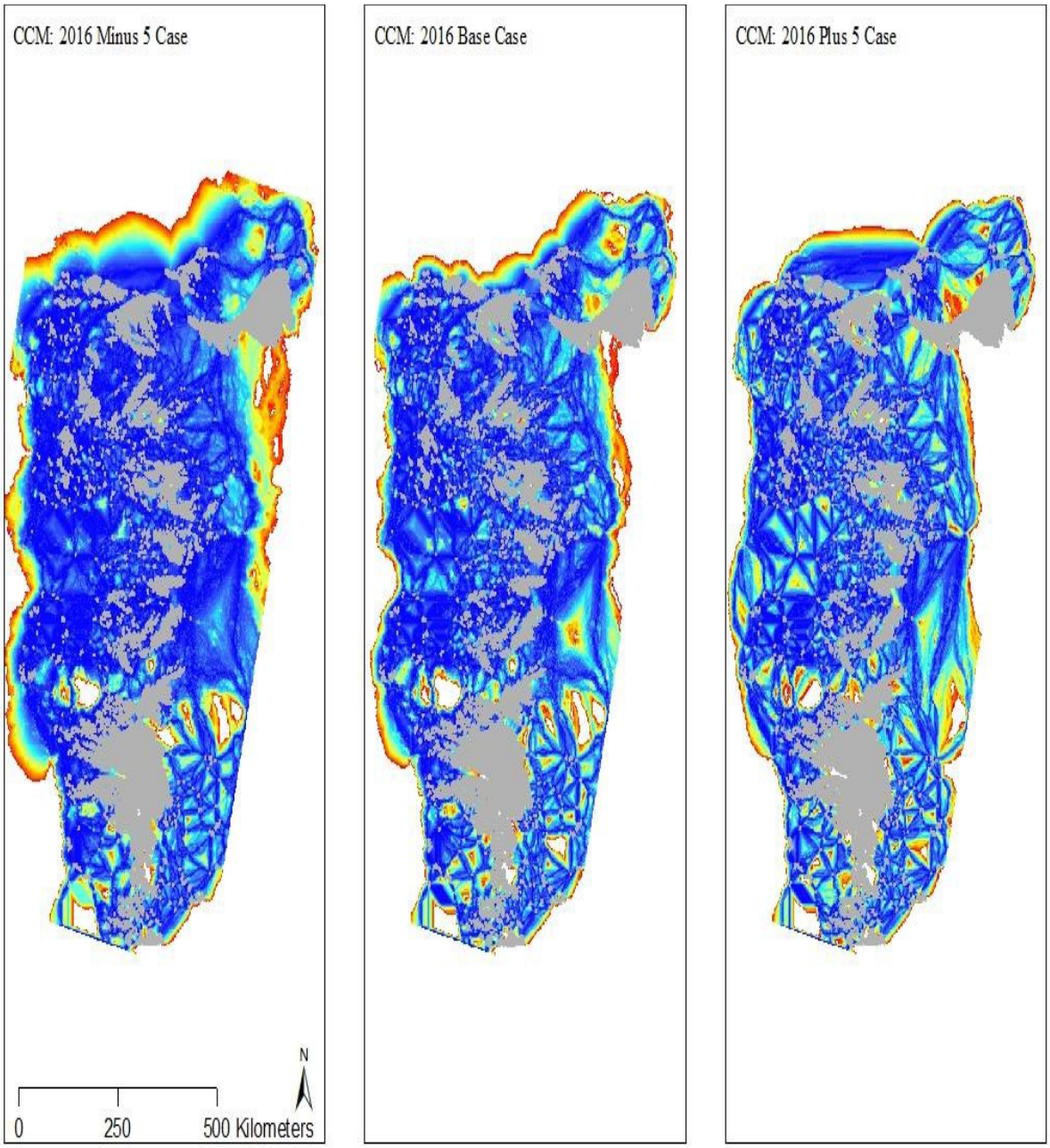

Figure 4.21. Landscape Resistance Modelling output of the Cropland Combined Model sensitivity analysis using the 2016 Minus 5 Case, the 2016 Base Case, and the 2016 Plus 5 Case. Areas of low resistance are in "cool" colors, and areas of high resistance are in "warm" colors, with playa wetland clusters in gray.

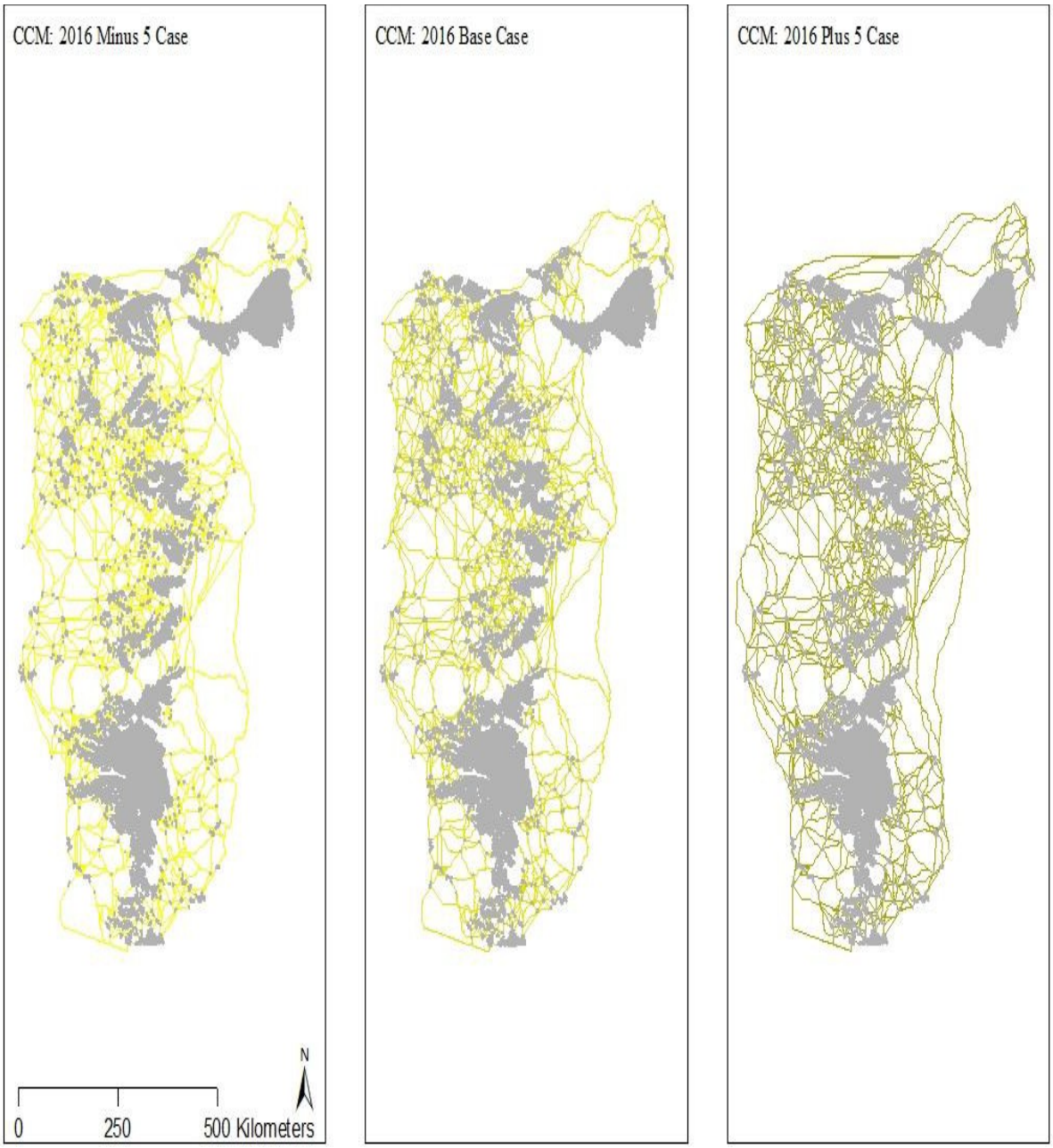

Figure 4.22. Least-Cost Path output for the Cropland Combined Model sensitivity analysis using the using the 2016 Minus 5 Case, the 2016 Base Case, and the 2016 Plus 5 Case. Yellow lines (shaded from light to dark, respectively) indicate locations of LCP linkages among playa wetland clusters in gray.

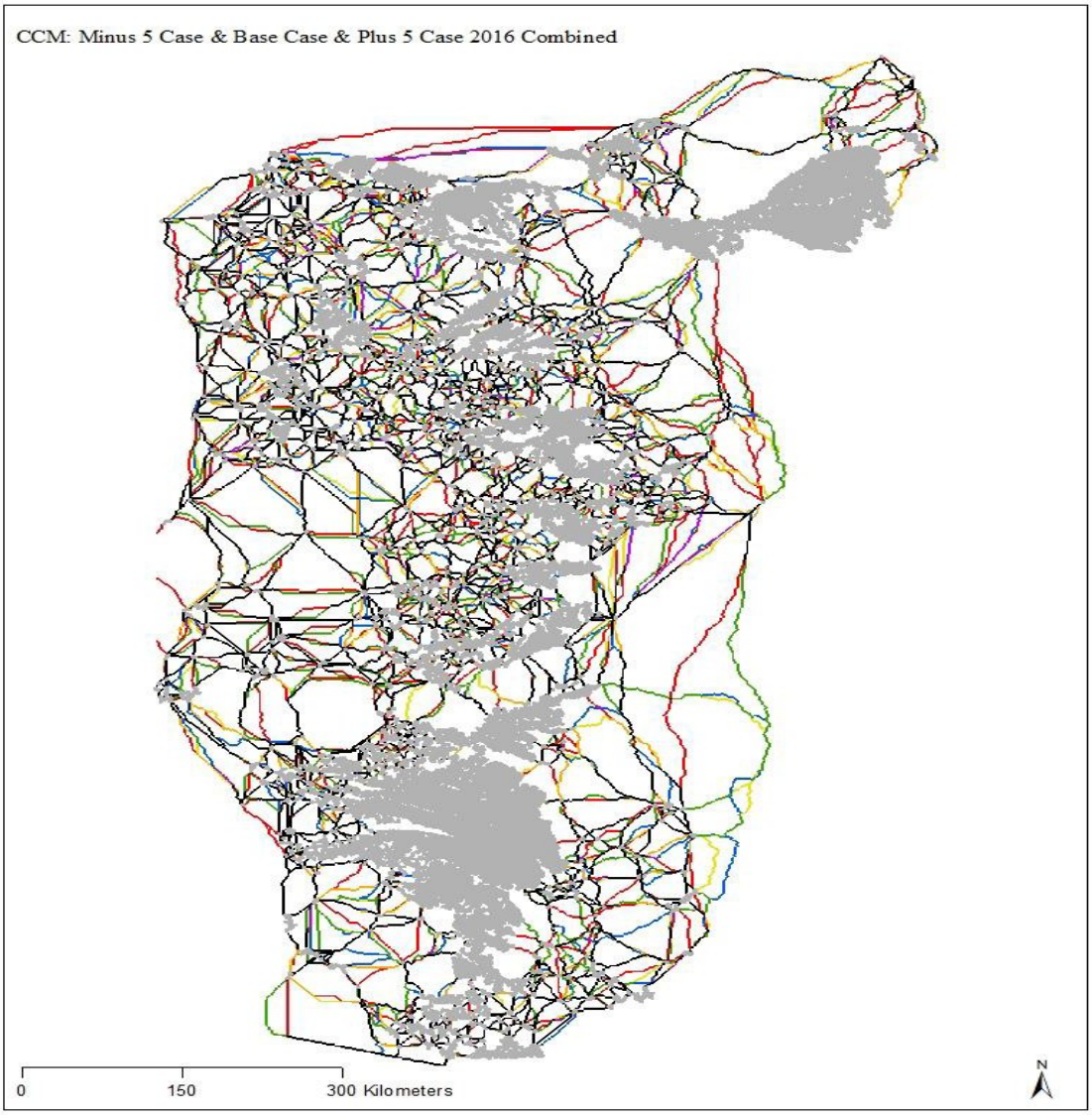

Figure 4.23. Combined Least-Cost Path locations for the Cropland Combined Model sensitivity analysis using the 2016 Minus 5 Case (blue lines), 2016 Base Case (yellow lines), and 2016 Plus 5 Case (red lines), with playa wetland clusters in gray. Least-Cost Paths locations overlapped 47% among the 2016 Minus 5 Case, 2016 Base Case, and 2016 Plus 5 Case (black lines), whereas 23% of remaining Least-Cost Paths overlapped with at least one other model (green lines: Minus 5 Case and Base Case Least-Cost Paths, orange lines: Base Case and Plus 5 Case Least-Cost Paths, purple lines: Minus 5 Case and Plus 5 Case Least-Cost Paths).

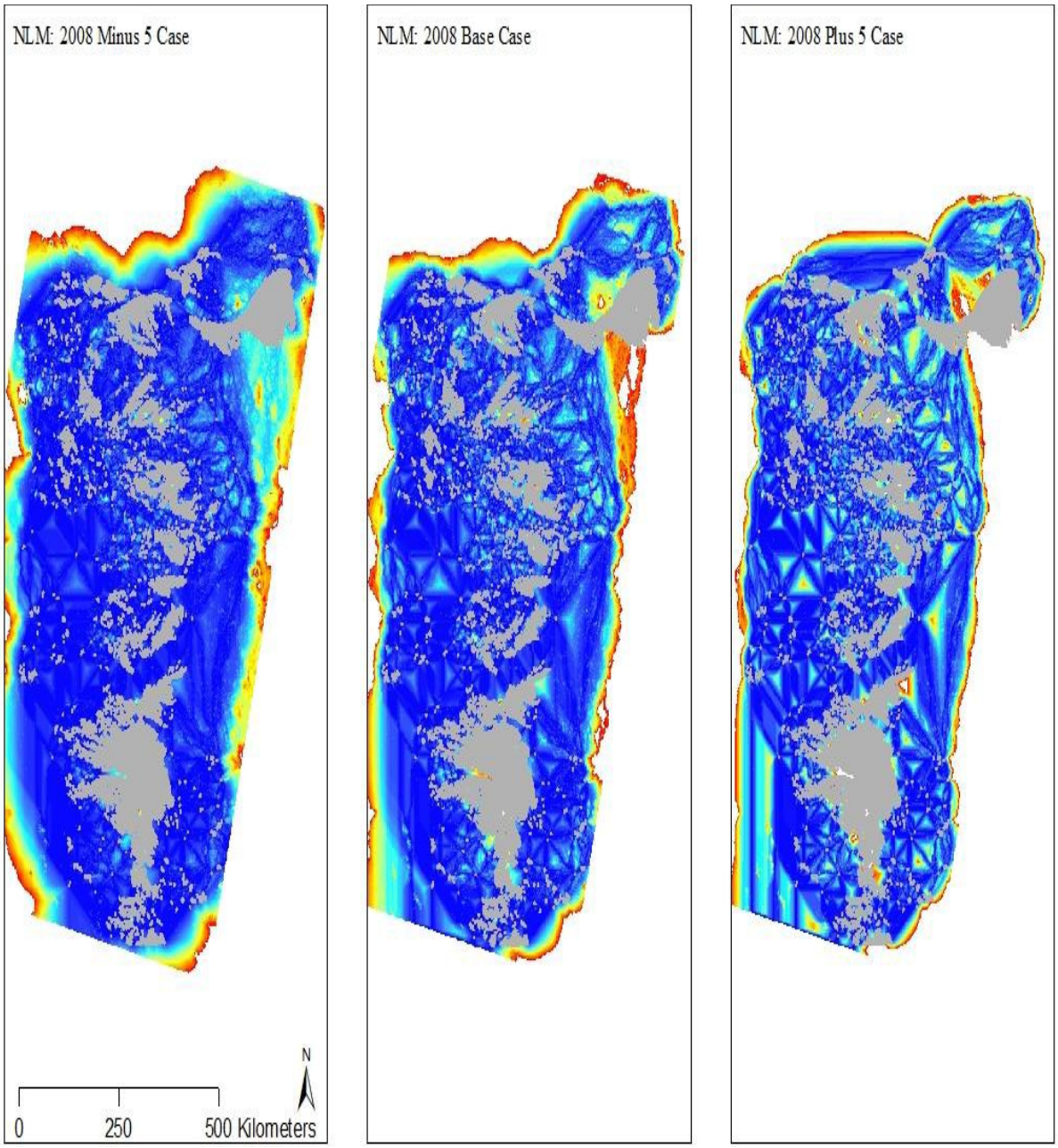

Figure 4.24. Landscape Resistance Modelling output of the Natural Lands Model sensitivity analysis using the 2008 Minus 5 Case, the 2008 Base Case, and the 2008 Plus 5 Case. Areas of low resistance are in "cool" colors, and areas of high resistance are in "warm" colors, with playa wetland clusters in gray.

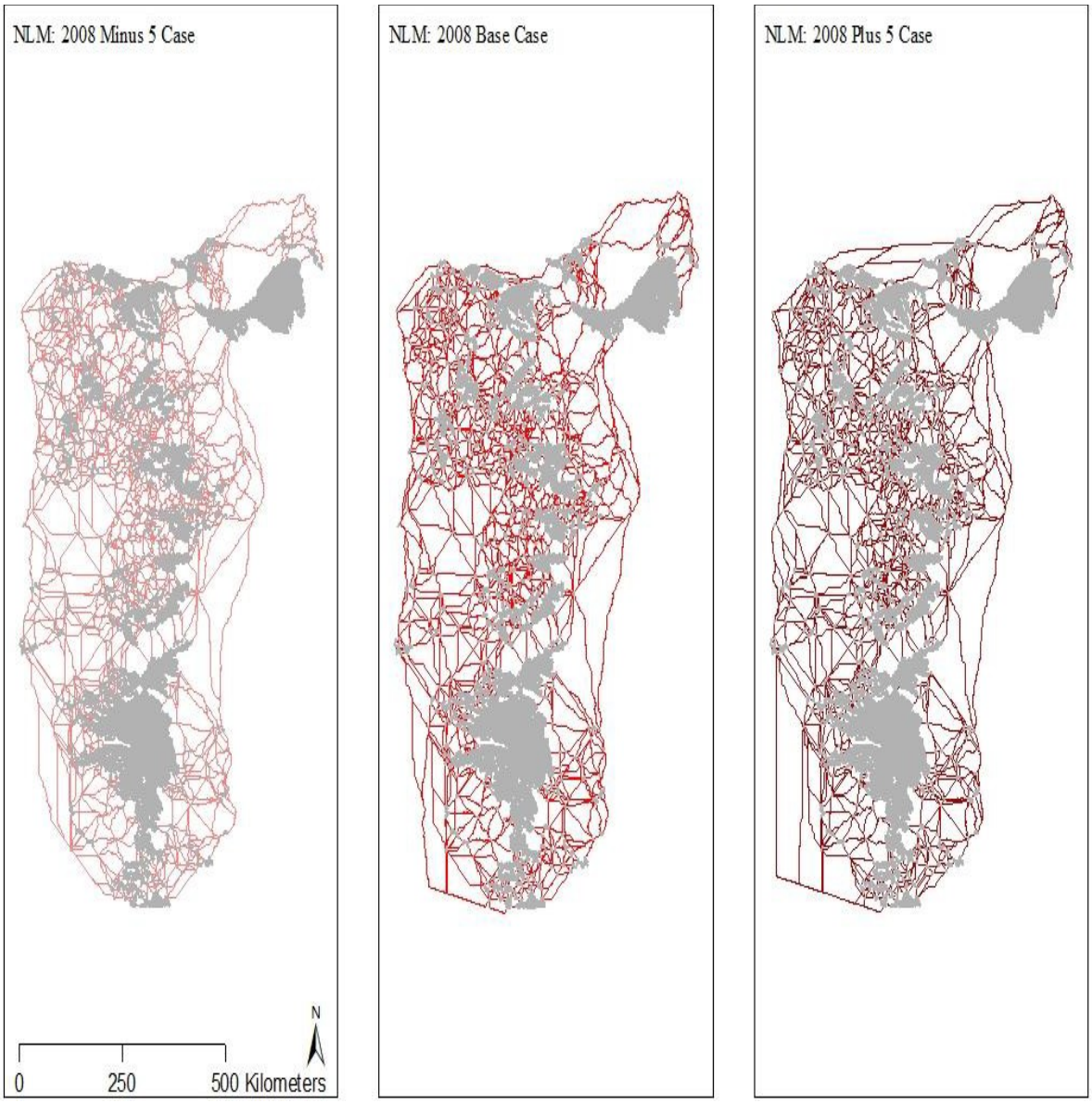

Figure 4.25. Least-Cost Path output for the Natural Lands Model sensitivity analysis using the using the 2008 Minus 5 Case, the 2008 Base Case, and the 2008 Plus 5 Case. Red lines (shaded from light to dark, respectively) indicate locations of Least-Cost Path linkages among playa wetland clusters in gray.

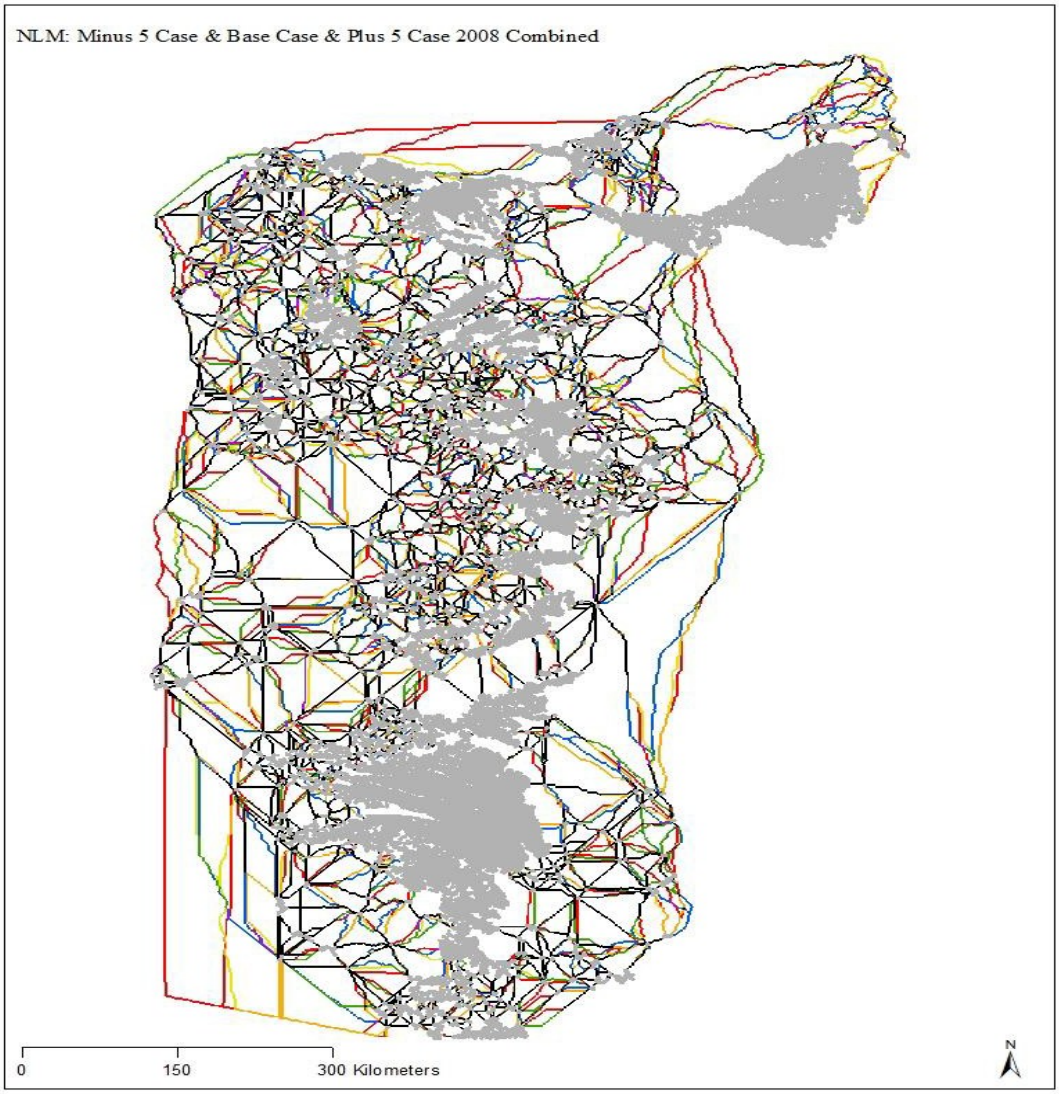

Figure 4.26. Combined Least-Cost Path locations for the Natural Lands Model sensitivity analysis using the 2008 Minus 5 Case (blue lines), 2008 Base Case (yellow lines), and 2008 Plus 5 Case (red lines), with playa wetland clusters in gray. Least-Cost Paths locations overlapped 44% among the 2008 Minus 5 Case, 2008 Base Case, and 2008 Plus 5 Case (black lines), whereas 23% of remaining Least-Cost Paths overlapped with at least one other model (green lines: Minus 5 Case and Base Case Least-Cost Paths, orange lines: Base Case and Plus 5 Case Least-Cost Paths, purple lines: Minus 5 Case and Plus 5 Case Least-Cost Paths).

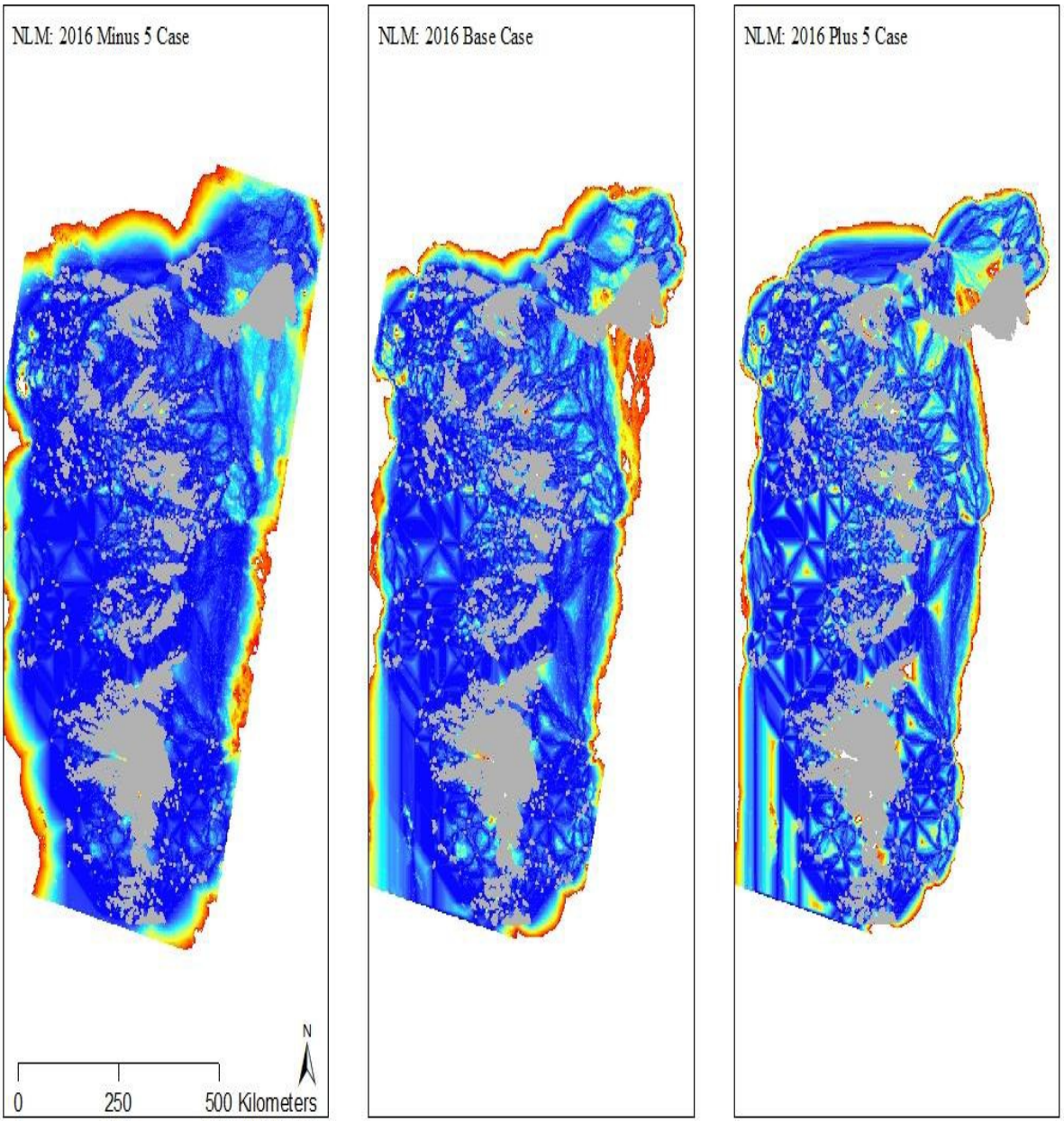

Figure 4.27. Landscape Resistance Model output of the Natural Lands Model sensitivity analysis using the 2016 Minus 5 Case, the 2016 Base Case, and the 2016 Plus 5 Case. Areas of low resistance are in "cool" colors, and areas of high resistance are in "warm" colors, with playa wetland clusters in gray.

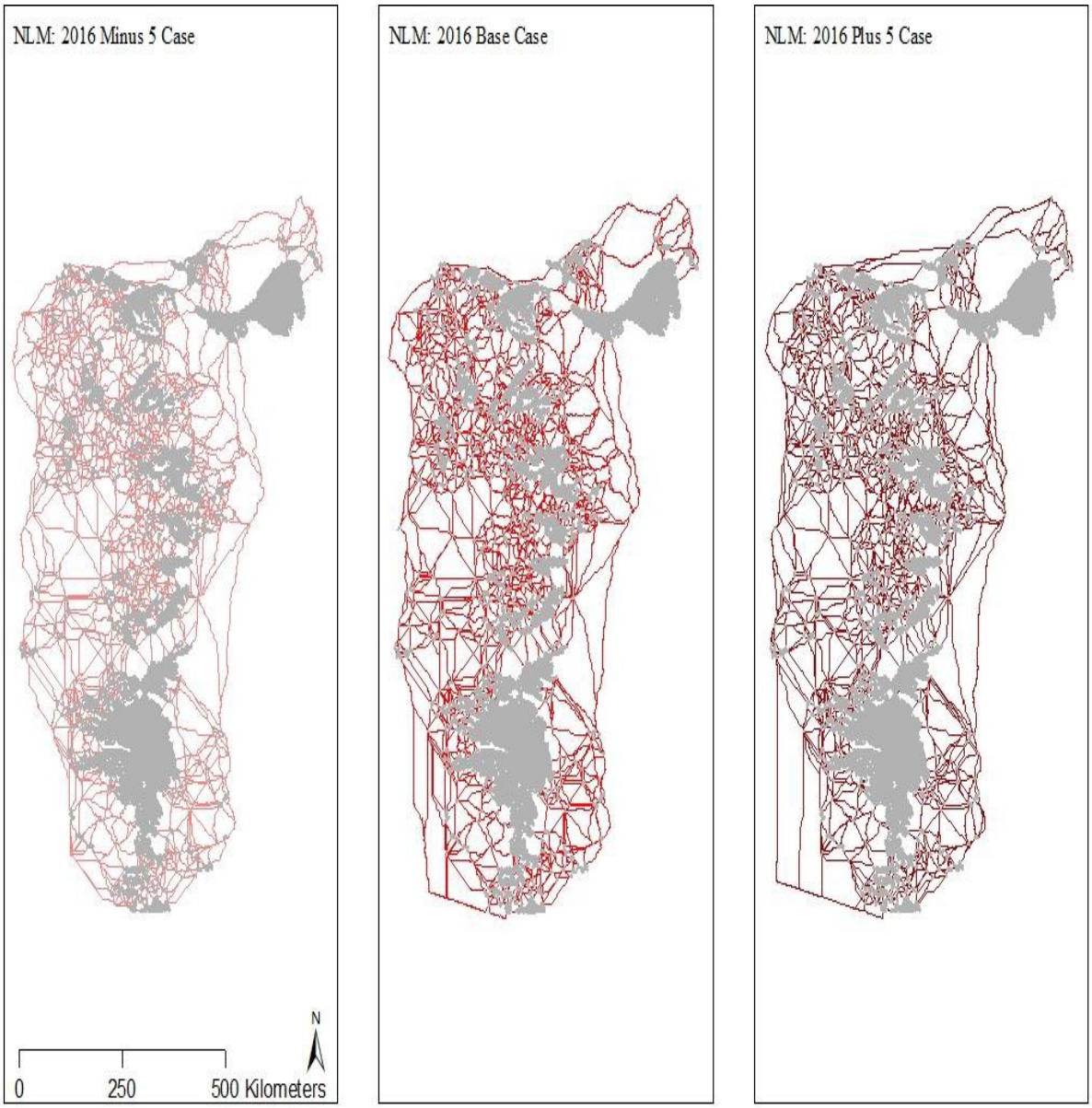

Figure 4.28. Least-Cost Path output for the Natural Lands Model sensitivity analysis using the using the 2016 Minus 5 Case, the 2016 Base Case, and the 2016 Plus 5 Case. Red lines (shaded from light to dark, respectively) indicate locations of Least-Cost Path linkages among playa wetland clusters in gray.

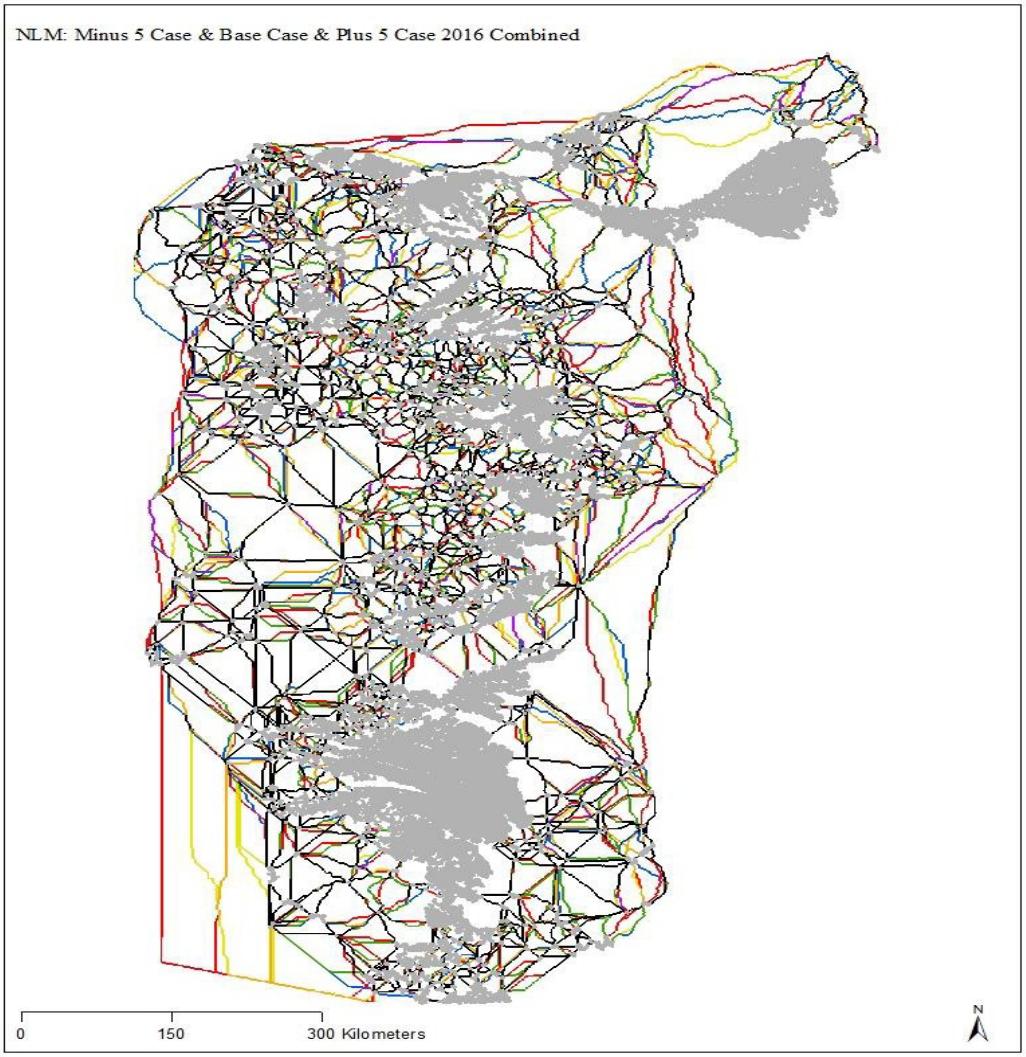

Figure 4.29. Combined Least-Cost Path locations for the Natural Lands Model sensitivity analysis using the 2016 Minus 5 Case (blue lines), 2016 Base Case (yellow lines), and 2016 Plus 5 Case (red lines) with playa wetland clusters in gray. Least-Cost Paths locations overlapped 44% among the 2016 Minus 5 Case, 2016 Base Case, and 2016 Plus 5 Case (black lines), whereas 23% of remaining Least-Cost Paths overlapped with at least one other model (green lines: Minus 5 Case and Base Case Least-Cost Paths, orange lines: Base Case and Plus 5 Case Least-Cost Paths, purple lines: Minus 5 Case and Plus 5 Case Least-Cost Paths).